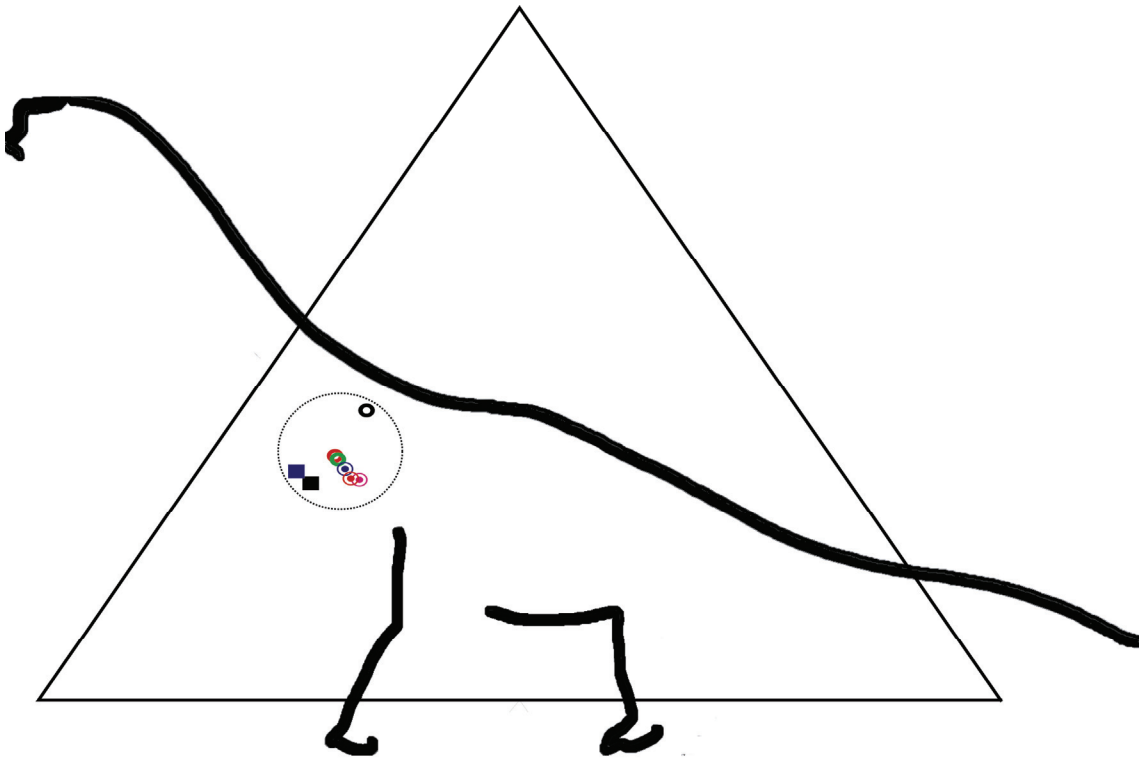
Sauropodomorpha (Dinosauria, Saurischia) appendicular skeleton disparity: theoretical morphology and Compositional Data Analysis



Luís Azevedo Rodrigues

Dissertation presented for the PhD degree in Sciences
with the Doctor Europaeus Mention

Unidad de Paleontología, Departamento de Biología.
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Doctoral Thesis

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Tese Doutoral

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Dissertação apresentada para a obtenção do grau de Doutor em Ciências com menção de Doctor Europaeus

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Dedicado a:

Aos meus Pais, irmãos e sobrinhos

À Maria

À minha família não-biológica: os meus amigos, nos quais incluo Ángela Delgado Buscalioni

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Contents/*Conteúdos*

Abstract

The appendicular skeleton of Sauropodomorpha was used as analysis object in a comparative context, along with other groups of Archosauria and Mammalia. The goal was to shed light on some aspects of the morphological evolution of Sauropodomorpha dinosaurs and, consequently, to explore some of the causes related to the mentioned morphological changes. Compositional data was obtained by measuring the length of several fore and hind limb elements and were employed and subsequently subjected to analytical methodologies based on Compositional Data Analysis (CDA). The database comprises about 600 entries and 2000 measured lengths.

The CDA statistical tools were thoroughly presented, reviewed and experimentally applied to different biological contexts, with the objective of testing their applicability before submitting our own data to this technique. The use of this methodological approach aims to contribute to a better knowledge of the appendicular geometry of Sauropodomorpha, but simultaneously to explore, under a macroevolutionary perspective, the quantification of disparity and proportions morphospace occupation patterns of the fore and hind limb extremities in a vast sample of Amniota.

Therefore, and based on CDA techniques, a new and rigorous morphospace disparity metric is proposed – Aitchison Distance, which in turn allows the quantification and discernment of the dissimilarities observed not only among a group, but also between different groups occupying proportions morphospaces, as well as the identification of the variability specific to each bone under scope. The assumption of size as a variable will permit the refinement of the global approach and, in some cases, the identification of its relation towards disparity.

Important questions, such as the changes in locomotion (from bipedalism to quadrupedalism) which took place in the evolutionary history of Sauropodomorpha and the gigantism issue unavoidable when focusing on some of the groups belonging to this clade are explored and interpreted under the scope of the CDA morphometric methodology. In order to better understand the amplitude of these changes, this study was extended to other dinosaur and mammal groups of bipedal and quadrupedal locomotion, and data concerning flying organisms was added to the analysis object, with the intent of creating a complete limb proportions morphospace integrating all of them: birds, bats, pterosaurs, theropods, ornithopods, artiodactyls, perissodactyls, carnivores and metatherians.

The structure of this work is organized as follows:

Chapter 1 (*Introduction/Objectives)* systematizes and contextualizes the conceptual and methodological backgrounds of this thesis, simultaneously relating them to its scientific objectives.

Chapter 2 (*Variation and Disparity metrics in ternary morphospace*s) presents and reviews the CDA analysis techniques which will constitute the methodological working tools of the analysis. The concepts of theoretical and empirical morphospace are reviewed, as is the concept of disparity. Some examples are used herein to corroborate the legitimacy and relevance of this analytical methodology regarding compositional data.

Chapter 3 (*Studies under Compositional Data Analysis – examples and re-analyses*) reanalyzes previously published works employing CDA techniques. Biological and conceptual contexts as diverse as the geometrical tools used in a macroevolutionary perspective focusing on the Archosauria cranium or the occupation of limb proportions

morphospaces in Pterosauria, Chiroptera and Aves are quantitatively reevaluated. Several analytical amplifications are performed, thus increasing and enriching the outcome results of the original researches, particularly concerning morphospaces occupation and disparity among flying tetrapods.

Chapter 4 (*Sauropodomorpha phylogenetic context and selected groups*) offers a revision of the phylogenetic hypotheses formulated regarding the clade Sauropodomorpha and describes the selection criteria presiding over the selection of the groups included in the performed morphometric analyses.

Capítulo 5 (*Sauropodomorpha locomotion - evolutionary history and appendicular skeleton morphology*) reevaluates some of the problematic issues concerning the appendicular skeleton morphological analysis of Sauropodomorpha: locomotion mode alterations regarding bipedalism and quadrupedalism, and also gigantism. The morphological characteristics of the diverse limb elements under analysis are also reviewed.

Chapter 6 (*Sauropodomorph Limb Disparity and Morphospaces*) explores the proportions morphospaces in Sauropodomorpha, the disparity quantifications concerning the several groups selected among the clade and the relation between size and disparity, and also introduces the relation between morphological integration and variability. The changes in the locomotion patterns are analyzed according to the morphospace occupation patterns by the diverse groups and according to the variability observed when focusing on the different limb elements.

Chapter 7 (*Dinosauria and Mammalia Limb Disparity and Morphospaces*) extends the methodological procedures already applied in chapters 3 and 6 to a much wider set of

animals, thus aiming to achieve an estimation of a global proportions morphospace of the appendicular skeleton. Variability and size are evaluated and thereafter both statistically and phylogenetically confronted, in order to attempt a depiction of bipedal and quadrupedal animal groups. Morphological integration levels are proposed for each group.

Sumário

O esqueleto apendicular de Sauropodomorpha foi usado como objecto de estudo num contexto comparativo, tendo-se igualmente utilizado outros grupos de Archosauria e de Mammalia. O objectivo é clarificar aspectos da evolução morfológica dos dinossauros sauropodomorfos e, consequentemente, explorar algumas das causas que originaram as referidas alterações morfológicas.

Utilizaram-se dados composicionais obtidos a partir dos comprimentos de distintos elementos do esqueleto apendicular anterior e posterior e aplicaram-se metodologias analíticas assentes na Análise de Dados Composicionais (CDA) numa base de dados de cerca de 600 entradas e 2000 dados métricos.

As técnicas estatísticas CDA foram detalhadamente apresentadas e revistas, aplicadas noutros contextos biológicos com o objectivo de testar a sua aplicabilidade, previamente à sua utilização na nossa base de dados. O uso deste enquadramento metodológico pretende contribuir para um melhor conhecimento da geometria apendicular de Sauropodomorpha mas tem simultaneamente o objectivo de explorar macroevolutivamente a quantificação de padrões de disparidade e de ocupação de morfoespaços de proporções das extremidades anterior e posterior para um conjunto amplo de Amniota.

Para este fim, e baseando-se em técnicas CDA, é proposta uma nova e rigorosa métrica de disparidade em morfoespaços - Distância de Aitchison, a qual permitirá quantificar e discriminar diferenças num grupo e entre distintos grupos nos morfoespaços de proporções, bem como identificar a variabilidade específica de cada elemento osteológico analisado. A incorporação da variável tamanho permitirá refinar e, nalguns casos, identificar a sua relação com a disparidade.

Questões como mudanças na locomoção (de bípede a quadrúpede) ocorridas na história evolutiva de Sauropodomorpha e o factor gigantismo inerente a

alguns grupos deste clado são exploradas e interpretadas segundo a metodologia morfométrica CDA. Para compreender a dimensão destas alterações, ampliou-se o estudo a outros grupos de dinossauros e a mamíferos, quer de locomoção bípede, quer de locomoção quadrúpede e foram incorporados na análise organismos voadores com o objectivo de configurar um morfoespaço completo das proporções das extremidades de todos eles: aves, morcegos, pterossauros, terópodes, ornitópodes, artiodáctilos, perissodáctilos, carnívoros e metatérios.

A organização do trabalho é a seguinte:

Capítulo 1 (*Introduction/Objectives)*, capítulo onde se sistematizam as bases conceptuais e metodológicas da presente Tese, bem como onde se formulam os objectivos.

Capítulo 2 (*Variation and Disparity metrics in ternary morphospace*s), neste capítulo são apresentadas e revistas as técnicas analíticas CDA que vão constituir o corpo metodológico das análises realizadas. Os conceitos de morfoespaço teórico e de morfoespaço empírico são revistos bem como o conceito de disparidade. Alguns exemplos biológicos são utilizados para comprovara a validade e a relevância desta metodologia analítica em dados composicionais.

Capítulos 3 (Studies under Compositional Data Analysis – examples and re-analyses), neste capítulo são reanalisados trabalhos previamente publicados com técnicas CDA. Contextos biológicos e conceptuais tão distintos como as bases geométricas num contexto macroevolutivo do crânio de Archosauria ou a ocupação de morfoespaços de proporções em Pterosauria, Chiroptera e Aves, são reavaliados quantitativamente. São efectuadas diversas ampliações analíticas e os resultados dos trabalhos originais

são incrementados e enriquecidos, em particular no que se refere aos morfoespaços e disparidade em tetrápodes voadores.

Capítulo 4 (*Sauropodomorpha phylogenetic context and selected groups*), neste capítulo é feita uma revisão das hipóteses filogenéticas propostas para o clado Sauropodomorpha e descrevem-se os critérios selectivos que foram seguidos na eleição dos grupos incluídos nas análises morfométricas realizadas.

Capítulo 5 (*Sauropodomorpha locomotion - evolutionary history and appendicular skeleton morphology*), neste capítulo é feita uma revisão de algumas problemáticas subjacentes à análise morfológica efectuada no esqueleto apendicular de Sauropodomorpha: alterações da locomoção bípede e quadrúpede, e o factor gigantismo. São igualmente revistas as características morfológicas de diversos elementos apendiculares que irão ser analisados.

Capítulo 6 (*Sauropodomorph Limb Disparity and Morphospaces*), neste capítulo procede-se à exploração dos morfoespaços de proporções em Sauropodomorpha, disparidade é quantificada para os diversos grupos seleccionados neste clado, a relação do tamanho com a disparidade é avaliada e é introduzida a relação entre integração morfológica e variabilidade. São analisadas as alterações nos padrões de locomoção baseando-se nos padrões de ocupação dos morfoespaços dos diversos grupos e em função da variabilidade observada nas distintas partes do esqueleto apendicular.

Capítulo 7 (*Dinosauria and Mammalia Limb Disparity and Morphospaces*), os procedimentos metodológicos aplicados nos capítulos 3, 6 são aqui ampliados para um conjunto mais amplo de animais, com o objectivo de alcançar uma aproximação a

um morfoespaço geral de proporções do esqueleto apendicular. Variabilidade e tamanho são avaliados e posteriormente confrontados estatística e filogeneticamente com vista a uma caracterização dos grupos animais bípedes e dos grupos animais quadrúpedes. Níveis de integração morfológica são propostos para os distintos grupos analisados.

Resumen

El esqueleto apendicular de Sauropodomorpha fue utilizado como objeto de estudio en un contexto comparativo, utilizando también otros grupos de Archosauria y de Mammalia. El objetivo es aclarar aspectos de la evolución morfológica de los dinosaurios Sauropodomorfos y, consecuentemente, explorar algunas de las causas que dieron lugar a los referidos cambios morfológicos. Se emplearon datos composicionales obtenidos de longitudes de distintos elementos del esqueleto apendicular anterior y posterior y se aplicaron metodologías analíticas utilizando como base los Análisis de Datos Composicionales (CDA) utilizando una base de datos de unas 600 entradas y unos 2000 datos métricos.

Las técnicas estadísticas de CDA han sido detalladamente presentadas y revisadas, aplicándolas en otros contextos biológicos con el objetivo de testar su aplicabilidad, previa a la utilización de nuestros datos. La utilización de este marco metodológico pretende contribuir a un mejor conocimiento de la geometría apendicular en Sauropodomorpha pero simultáneamente tiene el objetivo de explorar macroevolutivamente, la cuantificación de los patrones de disparidad y de ocupación de morfoespacios de proporciones de las extremidades anterior y posterior para un conjunto amplio de Amniotas.

Para esto, y basado en las técnicas CDA, se propone una nueva y rigurosa métrica de disparidad en morfoespacios - Distancia de Aitchison, la cual permitirá cuantificar y discriminar diferencias en un grupo y entre grupos distintos en los morfoespacios de proporciones y de identificar la variabilidad específica de cada elemento osteológico analizado. La incorporación de la variable tamaño permitirá refinar y, en algunos casos, identificar sus relaciones con la disparidad.

Cuestiones como los cambios de locomoción (de bípeda a cuadrúpeda) ocurridos en la historia evolutiva de Sauropodomorpha y el factor gigantismo inherente

a algunos grupos de este clado son exploradas e interpretadas según la metodología morfométrica de CDA. Para comprender la dimensión de estos cambios se amplió este estudio a otros grupos de dinosaurios y de mamíferos de locomoción bípeda y cuadrúpeda, y se incorporaron en el análisis datos de organismos voladores con el fin de configurar un morfoespacio completo de las proporciones de las extremidades de todos ellos: aves, murciélagos, pterossauros, terópodos, ornitópodos, artiodáctilos, perisodáctilos, carnívoros y metatérios.

La organización del presente trabajo es la siguiente:

Capítulo 1 (*Introduction/Objectives)*, es el capítulo donde se sistematizan y organizan las bases conceptuales y metodológicas de la Tesis, bien donde se formulan los objetivos.

Capítulo 2 (*Variation and Disparity metrics in ternary morphospace*s), en este capítulo se presentan y revisan las técnicas analíticas CDA que van a formar el cuerpo metodológico de los análisis. Los conceptos de morfoespacios teóricos y morfoespacios empíricos son revisados así como el concepto de disparidad. Algunos ejemplos serán utilizados para comprobar la validez y la relevancia de esta metodología analítica en datos composicionales.

Capítulo 3 (*Studies under Compositional Data Analysis – examples and re-analyses*), en este capítulo se reanalizan trabajos previamente publicados bajo las técnicas CDA. Contextos biológicos y conceptuales tan distintos como las bases geométricas en un contexto macroevolutivo en el cráneo de Archosauria o la ocupación de morfoespacios de proporciones en Pterosauria, Chiroptera y Aves, son revaluados cuantitativamente.

Se realizan diversas ampliaciones analíticas y los consecuentes resultados de los trabajos originales son incrementados y enriquecidos, en particular en lo que se refiere a los morfoespacios y disparidad en tetrápodos voladores.

Capítulo 4 (*Sauropodomorpha phylogenetic context and selected groups*), en este capítulo se hace una revisión de las hipótesis filogenéticas descritas para el clado Sauropodomorpha y se describen los criterios de selección que se han seguido en la elección de grupos que han sido incluidos en los análisis morfométricos realizados.

Capítulo 5 (*Sauropodomorpha locomotion - evolutionary history and appendicular skeleton morphology*), en este capítulo se hace una revisión de algunas problemáticas subyacentes en el análisis morfológico efectuado en esqueleto apendicular de Sauropodomorpha: cambios de locomoción bípeda y cuadrúpeda y el factor gigantismo. Y se revisan las características morfológicas de diversos elementos apendiculares que se van a analizar.

Capítulo 6 (*Sauropodomorph Limb Disparity and Morphospaces*), en este capítulo se procede a la exploración de los morfoespacios de proporciones en Sauropodomorpha, la disparidad cuantificada para los diversos grupos seleccionados en el clado, la relación del tamaño con la disparidad es evaluada y se introduce la relación entre integración morfológica y variabilidad. Se analizan los cambios en los patrones de locomoción basados en los patrones de ocupación de morfoespacios de los diversos grupos y en función a la variabilidad observada de las distintas partes del esqueleto apendicular.

Capítulo 7 (*Dinosauria and Mammalia Limb Disparity and Morphospaces*), los procedimientos metodológicos aplicados en capítulos 3 y 6 son aquí ampliados para

un conjunto de animales mucho más amplio, con el objetivo de obtener una aproximación a un morfoespacio general de proporciones del esqueleto apendicular. Variabilidad y tamaño son evaluados y posteriormente confrontados estadística y filogenéticamente con vista a una caracterización de grupos animales bípedos y animales cuadrúpedos. Niveles de integración morfológica son propuestos para los diversos grupos analizados.

1 - Introduction/Objectives

"It was not my opinion; I think there is no sense in forming an opinion when there is no evidence to form it on. If you build a person without any bones in him he may look fair enough to the eye, but he will be limber and cannot stand up; and I consider that evidence is the bones of an opinion."
Mark Twain**,** *Personal Recollections of Joan of Arc,* Chapter II (pp. 8–9)

"Phenotypic variation is the raw material for natural selection, yet a century after Darwin, it is an almost unknown subject."

Leigh Van Valen, 1978

"Variation is the *sine qua non* of biological evolution, providing the raw materials for sorting mechanisms such as natural selection and genetic drift. An understanding of variation (explicit or assumed) is essential for addressing virtually all paleontological questions."

Michael J. Ryan, *Encyclopedia of Dinosaurs*, p. 773

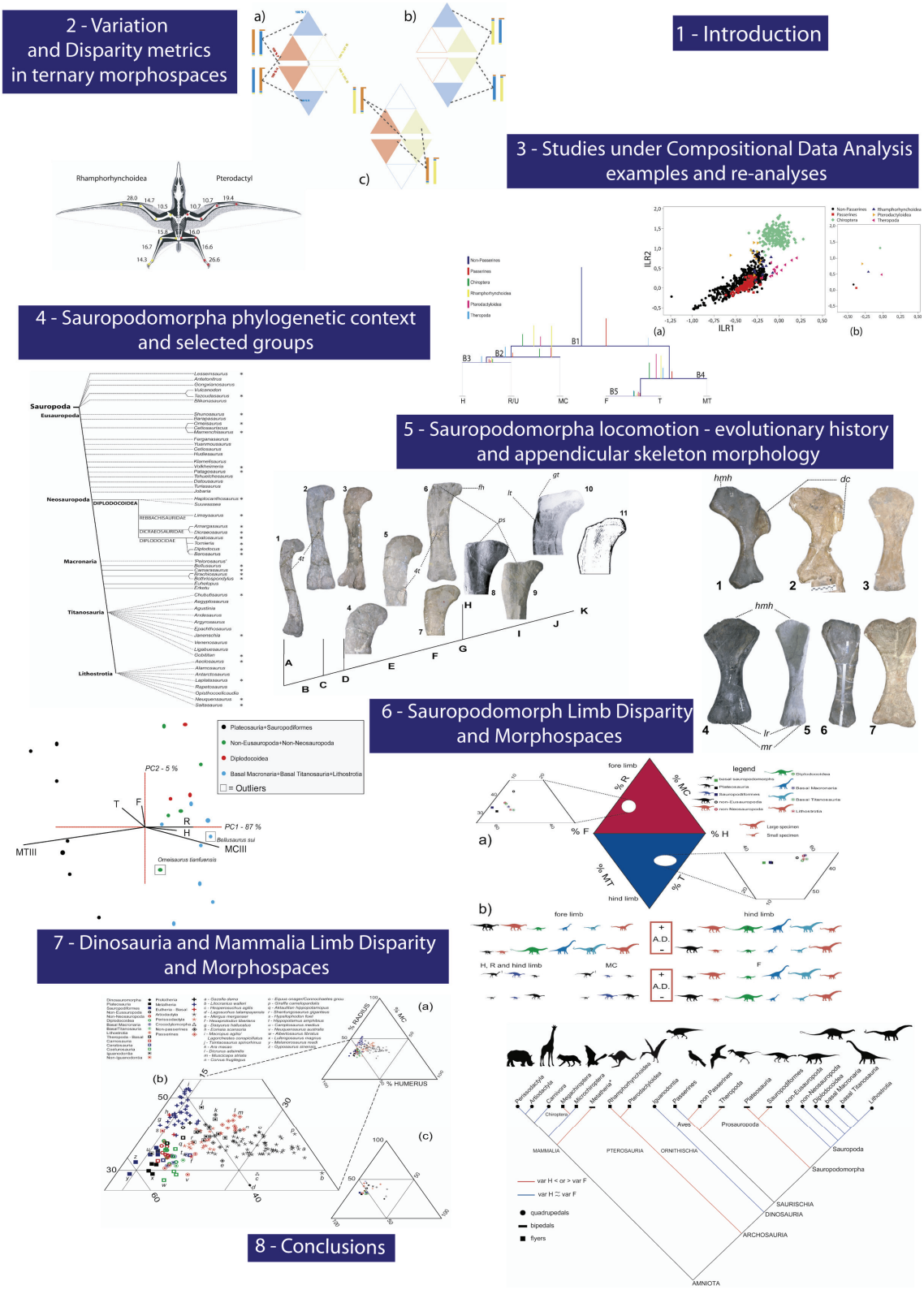

Figure 1.1 Thesis glance.

1. - Archosaurian limb disparity and locomotion. Archosauria have versatile locomotion patterns and were the first vertebrates with habitual bipedal posture (Sereno 1997).

Various and sometimes concurrent modes of locomotion arose among the large clade Archosauria: running, walking, sprawling, flying and swimming - all are movement types of these animals (e.g., Parrish 1986, 1987; Gatesy 1990, 1995; Carrano 1998a and b, 1999; Jones et al. 2000; Hutchinson and Gatesy 2000).

Even in particular archosaur groups such as Crocodylia, for example, locomotion exhibits different postures, like sprawling, belly walk, high walk and gallop, which in turn resulted in different and complex types of movement (e.g., Blob and Biewener, 1999; Parrish 1986, 1987, 1993).

Another locomotor innovation, responsible for most of the evolutionary success of a distinct archosaur group - Aves - is flight, which demanded the development of novel structures (feathers and other integumentary appendages), as well as the extreme adaptation of pre-existent skeleton features (e.g., Padian 1986, 1987; Sanz et al. 1996).

As for the Dinosauria clade, it presented a fully parasagittal gait in which the limbs were held beneath the body, a posture considered as primitive in this group (Padian 1997).

A non-archosaurian clade, Mammalia, has been herein analyzed with comparative objectives. The ancestors of mammals, mammal-like reptiles, developed an erect gait, although this posture has been firstly achieved in the hind limb (Kemp 1982) and they were all quadrupedals.

A comparative study on both mammals and archosaurs, concerning the limb proportions disparity by exploring morphospaces and rigorous Compositional Data Analysis (CDA) has never been performed. The studies by Romer (e.g., 1923, 1927) and Coombs (1978) somehow explored Archosauria and Mammalia limb proportions

and, particularly in the former, the interpretation of archosaurs locomotion types was based on morphological convergences with extant mammals. The referred work of Coombs also allowed to infer the locomotory capabilities of dinosaurs, for example, by comparing plots of the hind limb proportions (tibia : femur/metatarsal III : tibia) with those of living mammals. In the past 20 years, other works evaluated limb variation patterns among various groups of animals, using distinct statistical methodologies and resulting in morphological and functional analyses (e.g., Charig 1972, Norman 1980).

In the 1990's, distinct locomotor studies approaches were initiated by Gatesy (1990, 1995). These works put the emphasis on the use of distinct methods, such as phylogenetic, modeling, experimental and anatomical, in order to compile information and to produce a unique and robust inference of the function of a structure in fossil taxa.

One of the main objectives of the present work is to quantify and generalize, using numerical and statistical methods, the disparity of Archosauria appendicular skeleton, with special focus on Sauropodomorpha. Concomitantly, this work aims to establish a comparative framework and a methodological protocol allowing the inclusion of other tetrapods with great locomotor versatility, such as Mammalia, in separated or combined morphospaces (with Aves and Pterosauria, for example).

The inclusion of numerous and varied empirical group studies in the exploration of limb morphopaces was determined by the goal of creating a general limb morphospace. Similarly, in this context it is relevant to reassess the concept of locomotion pattern, complementing it with the generation of empirical morphospaces of proportions.

Based on the methodological framework proposed herein, locomotion patterns are the expression of locomotor areas deduced from both limbs empirical morphospaces. Generating these morphospaces permits to achieve distinct but complementary types of information, such as: quantification and location of occupied areas, limb parts variability within a group, disparity among groups and ranges of

occupation among clades at a macroevolutionary scale. All these types of information were applied in several generalizations and hypotheses that arise from the combined information of both limbs (fore and hind limb).

In order to fulfill the objectives of rigorously quantifying the empirical morphospace of proportions, which are constrained by the inherent and specific characteristics of the data, it was indispensable to introduce, from other scientific areas, statistical methods like the Compositional Data Analysis (e.g., Aitchison 1986; Egozcue et al. 2003; Egozcue and Pawlowsky-Glahn 2005, 2006). The majority of these methods will be introduced and described in chapter 2.

As a consequence of this methodological framework, the terminology of locomotion patterns is grounded in morphospace areas and limits. Due to the innovative character and original application of this methodology, the evolutionary implications of those morphospace areas and limits are not fully developed. In other words, distinct and detailed analyses would be required in order to combine and corroborate the morphological signals identified in the present work. This complementary approaches will be developed in future works and include, among other, Geometric Morphometric methods.

2.- The present work, as stated above, analyzes the selected bone parts proportions of fore and hind limbs. Both limbs could be interpreted as a “Modular Suprastructure” (MS) - *sensu* Rasskin (1995), which is organized through the articular conexion of parts, which constitute the descriptive units, and maintaining a clear relationship of homology within Tetrapoda (Shubin and Alberch 1986; Shubin et. al. 1997). The definition of Modular Suprastrucuture, in the present study, comprehends the sum of a selected number of preserved limb parts lengths. The cartilaginous component of the epiphysis was not considered in any case, neither the length component of the proximal carpals and tarsals. The study does not include any

elements of the pelvic or scapular griddles, since incorporating these elements could originate a methodological incoherence of elected proportions, because although connected limbs and griddles constitute distinct comparison axes.

Of each MS the stylopodium, one element of the zeugopodium (radius and tibia) and the elements of the distant tarsal belonging to the autopodium (third metacarpal and third metatarsal) will be examined. The selection criterion for one of the zeugopodium parts was mainly taphonomic, despite the biomechanically important role of the radius.

The following analyses are centered on the total length of each limb part. The data was obtained from published works (Dinosauria, Mammalia, Aves, Chiroptera, Pterosauria, Crocodylia), or personally measured (Prosauropoda, Sauropoda).

The objective is to identify and generalize variation patterns for each limb part among a clade or group established herein, as well as for the variation of each limb considered as MS. This framework has permitted to explore the relationship between fore limb vs. hind limb, giving attention to the comparison of equivalent elements, that is to say, stylopodium, zeugopodium and autopodium components of both limbs. This methodical perspective allows evaluating the existence of a tendency and/or the direction of variation patterns among fore or hind limb parts, or both.

3.- Limb proportions studies have been traditionally focused in differences on locomotion patterns and, analogously, disparity studies on the tetrapods appendicular skeleton have been strongly influenced by its function. This conventional view, at some extent perfectly plausible, was most of the times justified by the conception of limbs as very conservative body components in specific groups evolution, without a clear phylogenetic signal. A similar view assumes that the appendicular skeleton morphology is constrained by its locomotor mechanisms. Both points of view entailed that limb analyses were scarce and minimized in evolutionary studies.

This work analyzes in detail the following aspects: 1) locomotor convergences, reflected on the proportions of the appendicular skeleton parts - see chapters 3, 6 and 7; e.g., Pterosauria, Aves and Chiroptera; 2) the variation patterns among each analyzed group, in order to characterize the level of evolutionary stability. Special attention will be given to the evolutionary rarity of one specific mode of locomotion, flight and its appearance, known to have arisen only three times among tetrapods.

With these points of view in mind, few are the analyses in which shape and proportions are explored with a purely morphological emphasis. A fundamental object of the present work is the morphospace structure and occupation and, therefore, it will be centered on the morphological organization of the appendicular elements under the macroevolutionary concepts of disparity, phenotypic integration and modularity (e.g., Alberch et al. 1979; Maynard Smith et al. 1985; Gould 1989; Jablonski and Bottjer 1990; Erwin 1993; Zelditch and Fink 1996; Foote 1997; McGhee 1999).

Morphological Integration or the tendency of characters to covary is a field of studies initiated by Olson and Miller, who recognized its importance in evolutionary studies (1951, 1958). The patterns of covariation are used to infer underlying development of functional connections between traits. Olson and Miller's seminal work gave way to later developments, in particular by Cheverud (e.g., 1982, 1988, 1995, 1996). Among Cheverud's ideas, one can underline that genetic and phenotypic correlations are highly correlated, which in turn allowed to demonstrate that the phenotypic covariance structure can be applied as a proxy for the genetic covariance structure. Directly related with the present work's approach is Cheverud's opinion that there are three levels of morphological integration: functional and developmental integration (operating at an individual level), genetic integration (at a population level) and coordinated evolution of structures (at an evolutionary level).

Morphological integration related concepts are module and modularity. Works by Wagner (1995, 1996 a and b) and Magwene (2001) explored the concept of an

organism composed of semi-independent parts. These evolutionary concepts indicate that traits could be strongly related in terms of ontogeny or function.

The quantitative concept of disparity has been used in numerous macroevolutionary studies, as stated above. This numerical index is used as an indicator of "the spread or spacing of forms in morphospaces" (Eble 2005, p. 230) and reveals the phenotypic distinctiveness of a sample. Eble (2005) states that disparity could be considered as a general measure of variation and, in some morphological evolution problems, this concept could be interpreted as a proxy for trends in variational modularity. In the present study, this assumption of the relationship between disparity and modularity is applied in several sections, such as in the exploration of limb disparity and the absolute size - e.g., section 6.5 and chapter 7.

Disparity could be measured in numerous ways, but most often it is measured by "the total variance or the total range of *n* variables in a sample" (Eble 2004, p. 266). As can be concluded from the methodological procedures and analyses in chapters 2, 3, 6 and 7, this was the approach to the disparity definition herein favoured.

Modularity introduces the concept of organisms as hierarchical constituted levels, and of the phenotype as largely separable units in which the selection originates distinct and relatively independent biological responses. The organizational modularity (Eble 2005), by reflecting units of stability - organizational units, is associated to the interactions claimed to be important in organismal construction or activity. Variational modularity (Eble 2005), which reflects the magnitudes of interactions and their potential disruptions, could be detected from the variation and the covariation patterns of descriptive units, which in the present work are the limb parts. The present work morphometric variables, that is to say, the limb parts lengths and respective proportions, are considered to be variational morphological units. Eble (2004) denotes that variational modularity and disparity concepts could be associated, since "disparity

can be expected to be promoted by variational modularity, because modularity allows opportunities for semi-independent variation" (p. 266).

One will combine the measurement of variation and covariation as a numerical indicator of both modularity and morphological integration, which are, as seen above, related concepts.

A recent work by Mitteroecker and Bookstein (2007) systematizes some concepts and reviews diverse morphometric assumptions and methodologies in Morphological Integration and Modularity studies. These authors also tend to dissociate the cited evolutionary morphological concepts.

The study of variation in appendicular skeleton proportions of different taxa is initially grounded on the study of morphological disparity, which evaluates the phenotypical variation range of the selected elements. The disparity, defined in these terms, can be visually presented in a morphospace built on a ternary diagram. In this type of morphospace, statistical methods such as Compositional Data Analysis can also be applied - see below, in order to evaluate the statistical significance of the morphospace occupied areas for the analyzed taxa. The Aitchison Distance metric (A.D.) manifests, on its turn, a specific position, a distance among the morphological entities and, consequently, a formal definition of the areas occupied by the groups, as well as their limits in the morphospace.

Every chapter herein uses this methodological approach. At the end of this work, what could be considered as a general proportions morphospace is presented, in which the occupied areas are evaluated at a macroevolutive scale. In this general morphospace, the non-occupied but potentially occupied areas allow its definition in terms of disparity.

It is assumed that disparity analyses allow identifying distinct grades of limb parts proportions dominance, that is to say, a limb in which the stylopodium proportion clearly prevails (stylopodium dominated), or a limb in which the zeugopodium

proportion clearly prevails (zeugopodium dominated), or a limb in which the autopodium proportion clearly prevails (autopodium dominated). Once the morphospace occupied areas of a specific group are defined, one can investigate the variation patterns of each limb element within the defined suprastrucutre - fore limb, hind limb. This new variation analysis allows an estimation of the integration models that each analyzed group reveals. Morphological integration has been quantified through the analyses of biplots and balances - see chapters 3, 6 and 7.

Size - and its biological role - is one of the most relevant factors of a morphological analysis. The range of size among a certain clade or group elements could be considerable. The present work evaluates a probable relationship or constrains between size and the integration models of limb parts. This important biological feature is, for example, in the centre of the approach to Sauropodomorpha gigantism problem - see below and chapters 5, 6 and 7.

Although the anterior and posterior limb modules are explored separately in the ternary morphospaces, an organism is a deeper integrated unit. Therefore, one should expect that among the two limb units a combined variation pattern is observable and quantifiable. The testing of this hypothesis would have required a hexagonal morphospace (featuring the six limb parts of both limbs), but the statistical tools for this task are at the present time impracticable. Despite this methodological impediment, this work explores the combined variation of equivalent parts - fore limb vs. hind limb; humerus vs. femur, for example.

Concerning sauropodomorphs evolutionary history, Carrano (2005, p. 223) states that “most of the body-size increases occur early in sauropod evolution and were largely completed by the Upper Jurassic neosauropod radiation.” Carrano (2005) also

denotes that the cited body-size increase* was achieved in a small time interval in Neosauropoda, Macronaria being the only Sauropoda group that reveals a reduction in size. On the other hand, diplodocoids reveal an intensification of characteristic neosauropod body-size increase.

Taking these trends into account, one has verified that both extremes of the Sauropoda clade reveal identical relationship of size and hind limb proportions disparity, that is to say, non-eusauropods and lithostrotians smaller species reveal higher proportions disparity than this groups bigger species – see section 6.8.

4.- Although a connection between limb parts proportions and an organism locomotion patterns are clear but not completely evident, due to other biomechanical factors that characterize and limit the limbs function (e.g., the axial skeleton and associated musculature), a referential method is required that allows to establish a rigorous comparison between distinct biological entities.

In chapter 3, a sample of flying tetrapods was revised, namely birds, bats pterosaurs. This limb parts dataset has been analyzed by other authors in a compositional framework, but without applying any of the Compositional data Analysis used herein.

This is the first time that these analytical techniques have been used in this kind of in flying tetrapods and with the purposes of identifying morphospace occupation patterns besides quantifying wing disparity. Previous works focused in similar questions but lacked the CDA approach herein presented (Gatesy and Dial 1996; Gatesy and Middleton 1997; Middleton and Gatesy 2000; Dyke et al. 2006; Mcgowan and Dyke 2007).

* "Not surprisingly, early sauropod evolution is characterized by a steady increase in body size from the condition seen in [basal sauropod] *Vulcanodon* and larger prosauropods to that in basal neosauropods, representing at least a doubling in size over some 40 million years…" Carrano 2005, p. 231.

The sample included numerous specimens of Aves (Passerines and non-Passerines), Chiroptera (Megachiroptera and Microchiroptera) and Pterosauria (Rhamphorhynchoidea and Pterodactyloidea) – see table 3.10.

The Compositional Data Analysis included the construction and the numerical description of both fore and hind limb morphospaces; the quantification of disparity (Aitchison Distance) within and among the groups; and the identification of disparity outliers, as well as the performance of statistical tests on the limb parts proportions.

5.- The study of disparity and integration in Sauropodomorpha limb parts, as in other archosaurian and non-archosaurian groups, is performed in chapters 6 and 7. Sauropodomorphs are analyzed within a phylogenetic context, and the studied species were grouped abiding by partially paraphiletic criteria, that is to say, employing phylogenetic hierarchy the groups singularize the descendents, in some cases, while in others they exclude the descendents. For example, Sauropoda terminal clades like Lithostrotia constitute a monophyletic group, while the grouping of Titanosauria excludes the hierarchical superior clade Lithostrotia, constituting in this case a paraphyletic group. This phylogenetic referential allows, despite the use of paraphyletic groups, to perform comparisons among distinct paraphyletic groups that constitute a monophyletic node.

In general terms, the most evident differences within the limb parts proportions are centered in large clades. In chapter 4 the criteria for this grouping is justified. The selection of the phylogenetic context allows exploring two of the most interesting aspects of Sauropodomorpha evolution: the quadrupedal or bipedal condition of this clade and the hypotheses related with the gigantism in sauropods. A general and brief introduction to this biological problem is made in chapter 5.

The present study also performs a morphological characterization of the analyzed limb parts, taking into account the selected groupings, developed in detail in chapter 4.

In addition, distinct levels of limbs morphological organization were illustrated, in such a way that not only the morphological analysis of the mere parts is performed, but also, at a higher level, of the limb parts proportions that constitute a modular suprastrucuture.

Epistemologically, morphology studies reveal different levels of information. Although traditional shape analysis does not reveal substantial morphological differences in limb parts among the distinct species of the clade Sauropodomorpha, the limb parts proportions analyses revealed a different reality.

A stronger support of this statement could be attained by extending the shape analysis to the most meaningful proportions, with a Geometric Morphometric study, in 2D or 3D. This combination of distinct levels of morphological information would allow us “to efficiently assess patterns of form.” (Rasskin 2003, p. 306). Although the exploration of the “Boundary Constraints” concept (Rasskin 2003) has not been explored in this work, this idea is suitable for the biological type and compositional data used herein.

Surprisingly, size has a unique role in the results interpretation of this study. Traditionally, proportions have been interpreted as being the result of the relationship of size and shape, but have never been explored separately. The results presented in chapters 6 and 7 show how size can be understood as a variable that is independent of proportions. The size factor was removed by comparing limb parts proportions and thereafter comparing the disparity metrics of that compositional data with the absolute size.

6.- In chapters 6 and 7 the proposed methodological framework is reviewed and described in detail, in order to examine the extent of the results achieved, which are associated with the mentioned biological questions: the evolutionary locomotor changes in Sauropodomorpha and its association with size.

The results attained in these chapters could be interpreted in three ways: the characterization of the evolutionary novelties between clades, in terms of proportions and variation of appendicular skeleton parts; the convergences among the different analyzed groups; the analysis of shape as a vital constrain factor of proportions of the appendicular skeleton parts.

The disparity analyses show that Sauropodomorpha designated locomotor patterns are not simple and immediately identifiable but, instead, far more complex than a mere assignment to a dual bipedal - quadrupedal model.

In the general morphospace of mammals and archosaurs, sauropodomorphs are positioned in a particular area, which is defined by the dominance of the humerus in the fore limb and of the femur in the hind limb. Although the analogy of sauropods with elephants is recurrent, in traditional approaches (Holland 1910; Bakker 1971) or more recent ones (e.g., Hutchinson 2008), the present work demonstrates that the comparison is more evident in the hind limb than in the fore limb.

The prosauropod scenario is somewhat different and singular, since it occupies an extreme morphospace area, particularly in the fore limb, but in no case its position is somewhat comparable to the assumed “bipeds”. Prosauropods singularity could be characterized, in the fore limb, by the dominance of the humerus, comparatively to sauropods, which exhibit a shared dominance of stylopodium and zeugopodium.

One of the most intriguing results is that the analyzed groups’ distribution within the proportions morphospace does not preserve any relationship with its morphological or biomechanical organization. In general terms, one can distinguish a

typical mammalian area in which higher disparity is explored and an archosaurian area, more limited, although with some overlapping regions with mammals in a way that allows the identification, for example, of minimum distances between dissimilar groups (in the fore limb) like Ornithischia and Perissodactyla and higher distances between Ornithischia and Sauropodomorpha.

Ternary morphospaces, due to its intrinsic properties, allow to discern detailed areas which, therefore, quantitatively determine micro-spaces occupied by groups. Specific groups like Sauropoda could be characterized by its proportions and, in groups with considerable disparity, such as Perissodactyla, the biological meaning of that dispersion could be explored, relating it with the groups' evolutionary history or taxonomy.

The study of proportions morphospaces *per se*, despite being applied as a tool for revealing change trends in proportions, does not fully achieve the necessary resolution level required for answering some evolutionary questions, such as which are the morphological constrains for bipedality or quadrupedality among clades or even macroevolutionary. Therefore, the motivation for exploring proportions through the quantification of the variability of limb parts proportions originates a higher level of morphological information.

The variation analyses herein performed allow to estimate the integration models inherent to a group under a phylogenetic perspective (clades) or under an adaptative perspective (convergent models) – see chapters 6 and 7. The integration models include identifying trends in variation across homologue modules such as fore and hind limbs or humerus and femur. In Sauropodomorpha, largely, but also in other groups, namely in other dinosaurs and Mammalia, the level of variation of each bone part in the fore limb, hind limb or the relation of bone parts across limbs are explored. For example, the Sauropoda node could be defined as the one, among Sauropodomorpha, in which the variation pattern among the three parts of the hind

limb is at its maximum. Complementarily, the variation patterns also reveal that the Macronaria fore limb is the most variable, if one compares the proportions of the humerus and of the radius against the metacarpal. If one considers humerus-radius variability as an evolutionary novelty within Sauropodomorpha, one should expect the existence of a correlation between morphology and the proportions. These are the sort of issues hereby raised which will yield future research fields.

The information regarding integration models can be obtained through the results of Biplots variance and Balances analysis - see chapters 2, 3, 6 and 7. The Balances methodology permits, through the graphic illustration (dendrogram) of a sequentially binary partition of the variance, the revealing of evolutionary trends in the appendicular skeleton parts of Sauropodomorpha. For example, a reduction in variation of the humerus could be identified when compared to the radius in Sauropoda.

Under an adaptative perspective, a more detailed study of the variation among equivalent elements in the fore and hind limbs clearly allows to delimitate an integration model in prosauropods and sauropods. The former sauropodomorphs exhibit low integration among both limbs, as the result of high variation between fore and hind limbs, corroborated by the high variance differential of humerus and femur. In modularity terms, it could be suggested that the limb modules are biomechanically independent. On the other way, there are modules which are biomechanically dependent, such as the limbs among Artiodactyla, Perissodactyla, Carnivora or Iguandontia, in which there is low variation between fore and hind limbs - see section 7.10, table 7.9 and figure 7.10.

The combination of variations extracted from Balances analyses and the Biplots variances of both limbs will constitute the core for the bipedal or quadrupedal definition. A bipedal could be defined as an organism in which the fore limb is decoupled from the hind limb, being the quadrupedals defined as an organism in which both limbs variations are associated.

The starting point in this study was to show that the integration of fore and hind limbs among bipedal forms is lower than the integration among quadrupedals. One of the aimed objectives is to comprehend and evaluate the number of organizational plans among bipedal forms, since prosauropods manifestly contrast theropods, birds, anthropomorphic primates or kangaroos. This framework will allow the opportunity to test functional or biomechanical hypothesis that implicate other structures in locomotion. It is reasonable to believe that some of this work's results will permit to produce new work hypotheses in which one considers the level of integration of each limb with the corresponding gridles or musculoskeletal regions functionally associated to them.

Size is another significant biological question in the evolutionary history of Sauropodomorpha. It plays a key role in the appendicular skeleton disparity, and this statement implies that the size of the complete limb (fore or hind limb) is in some way related to the morphospace occupied range areas.

One could quantify the disparity (Aitchison Distance) and relate it to the absolute limb size. Nonetheless, this relation is constrained by phylogeny, in a way that evolutionary trends in Sauropodomorpha could be identified, despite the fact that opposite trends could arise in fore and hind limbs. Regarding this, Neosauropoda fore limb shows an inverse relationship between AD and size, that is to say, bigger neosauropods present a narrower dispersion in the fore limb morphospace. Since the variation in Sauropoda hind limb is considerable higher, and although it could be identified in certain groups, there is no clear and generalized trend. The evolutionary path of gigantism in Sauropodomorpha involves, this way, and as will be verified in chapter 6, two patterns of sauropods fore limb morphospace occupation that can be defined as follows: one for basal sauropods (bigger specimens have higher disparity indexes) and another for derived sauropods (bigger specimens have lower disparity indexes). As stated above, and in order to deepen the morphological characterization

of the gigantism path in Sauropoda limbs, it is necessary to complement the proportions analyses with other sort of morphological studies, like geometric morphometrics. For example, the humerus of the saltasaurids (derived macronarians) shows unique morphological features, such as the prominent deltopectoral crest and the distal condyles, divided and exposed anteriorly (Wilson 2005). Together with other morphological particularities, such as in the ulna and the increased transverse diameter of the distal radius, they allow to infer that saltasaurids have a more flexed forelimb posture. The cited morphological changes could be confronted with morphospace disparity metric in order to achieve a clear view of this terminal group's limb evolution trajectory.

7 - the methodological framework proposed in the present study has disclosed a considerable number of further research areas: estimation of missing values in the fossil record through CDA; analysis of the particular conditions of the identified outliers; reconstruction of juvenile specimens disparity; study of the relation between morphological integration and size, through Balances and variation analyses.

1 - Introdução/Objectivos

"It was not my opinion; I think there is no sense in forming an opinion when there is no evidence to form it on. If you build a person without any bones in him he may look fair enough to the eye, but he will be limber and cannot stand up; and I consider that evidence is the bones of an opinion."
Mark Twain**,** *Personal Recollections of Joan of Arc,* Chapter II (pp. 8–9)

"Phenotypic variation is the raw material for natural selection, yet a century after Darwin, it is an almost unknown subject."

Leigh Van Valen, 1978

"Variation is the *sine qua non* of biological evolution, providing the raw materials for sorting mechanisms such as natural selection and genetic drift. An understanding of variation (explicit or assumed) is essential for addressing virtually all paleontological questions."

Michael J. Ryan, *Encyclopedia of Dinosaurs*, p. 773

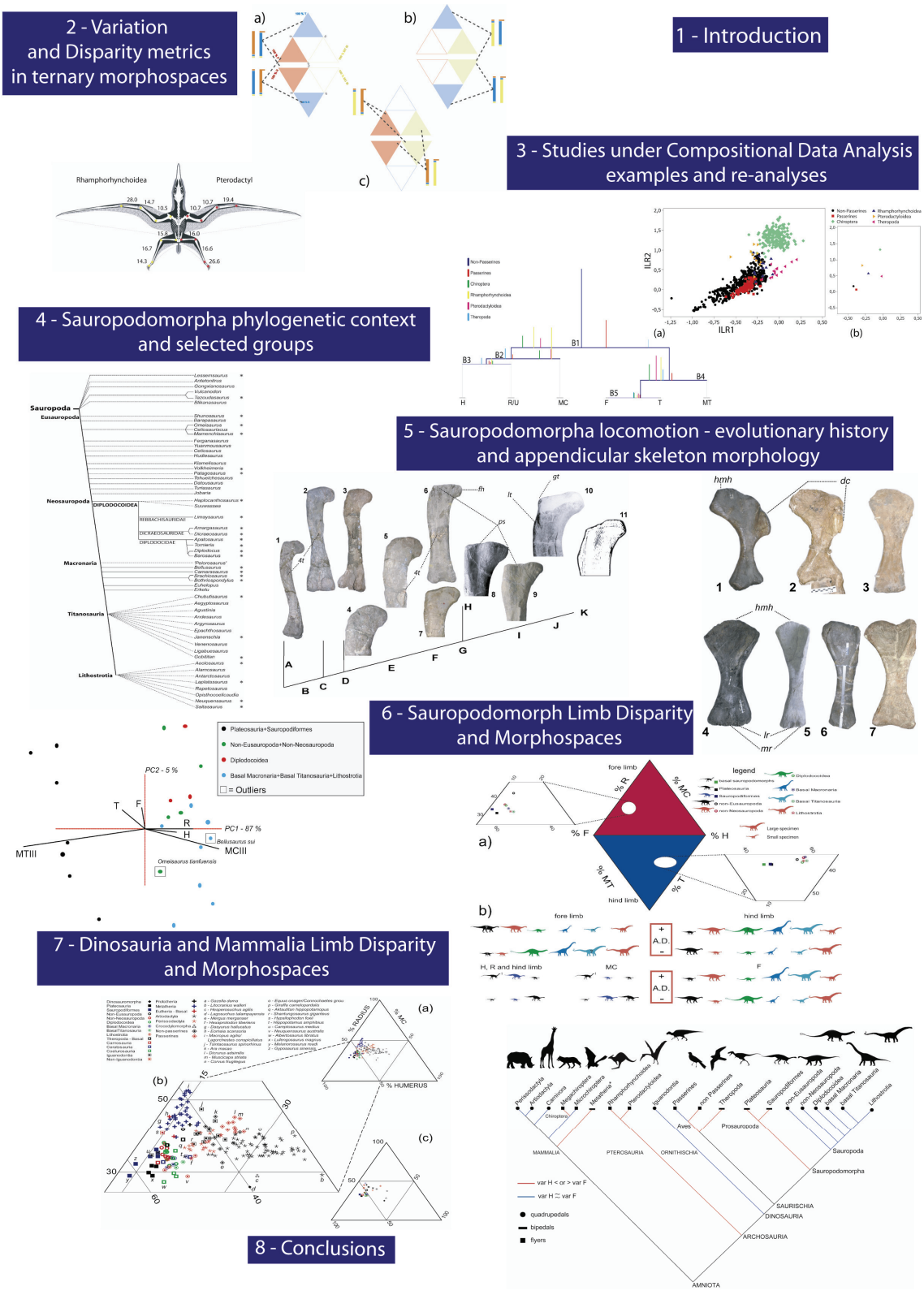

Figura 1.1 A Tese num relance.

1. - Disparidade e locomoção em Archosauria. O clado Archosauria apresenta padrões de locomoção com grande versatilidade, tendo sido os primeiros vertebrados com uma postura bípede obrigatória (Sereno 1997).

Foram diversas as formas de locomoção que surgiram simultaneamente por entre os membros deste vasto clado: corrida, caminhada, rastejamento, voo e natação - todos são tipos de deslocação utilizados por estes animais (cf. p.e. Parrish 1986, 1987; Gatesy 1990, 1995; Carrano 1998a and b, 1999; Jones et al. 2000; Hutchinson and Gatesy 2000).

Mesmo em grupos particulares de arcossauros, como Crocodylia, por exemplo, a locomoção apresenta diversas posturas corporais: rastejamento, locomoção de ventre rente ao chão ("belly walk"), locomoção com membros em postura parassagital, ou seja, paralelos e completamente erguidos sob o corpo, suportando-o ("high walk") e galope, as quais, por sua vez, conduzem a distintos e complexos tipos de deslocação (cf. p.e. Blob and Biewener, 1999; Parrish 1986, 1987, 1993).

Outro tipo de inovação ao nível da locomoção, responsável pelo sucesso evolutivo de um outro grupo de arcossauros – Aves – é o voo, o qual exigiu o desenvolvimento de estruturas anatómicas inéditas (penas e estruturas tegumentárias não-ramificadas, por exemplo), bem como uma adaptação radical das características osteológicas preexistentes (cf. p.e. Padian 1986, 1987; Sanz et al. 1996).

O clado Dinosauria apresentava uma postura parassagital completa, na qual os membros estavam posicionados sob o plano corporal, postura considerada como primitiva neste grupo (Padian 1997).

Um clado não-arcossauriano, Mammalia, foi utilizado neste trabalho como termo de comparação. Os antepassados dos mamíferos, os répteis mamaliformes, eram quadrúpedes e desenvolveram uma postura erecta que, todavia, foi adquirida primeiramente no membro posterior (Kemp 1982).

Este tipo de estudo comparativo, integrando simultaneamente mamíferos e arcossauros, focando a disparidade das proporções dos membros e uma rigorosa Análise de Dados Composicionais (CDA), não foi anteriormente efectuado. Os trabalhos de Romer (cf. p.e. 1923, 1927) e de Coombs (1978) exploraram, em certa medida, as proporções dos membros de Mammalia e de Archosauria. Em especial no que se refere ao primeiro autor, a interpretação dos tipos de locomoção em arcossauros baseou-se em convergências morfológicas com os actuais mamíferos. Já os trabalhos de Coombs permitiram, por sua vez, inferir a capacidade locomotora dos dinossauros, por exemplo através da comparação das proporções dos membros posteriores (tíbia : fémur/metatarso III : tíbia) com informação equivalente de mamíferos actuais. Nos últimos vinte anos, outros trabalhos procuraram avaliar padrões de variação nos membros de vários grupos de animais, aplicando metodologias estatísticas que conduziram a análises morfológicas e funcionais (cf. p.e. Charig 1972, Norman 1980). Na década de 90 do século passado, vários estudos e métodos de análise de locomoção foram propostos por Gatesy (1990, 1995). Estes trabalhos enfatizaram a utilização de variadas metodologias, tais como a filogenética e a modelação experimental ou anatómica, com vista a compilarem informação e a formarem inferências sólidas e singulares sobre a função locomotora em grupos fósseis.

Um dos objectivos principais do presente trabalho é quantificar e generalizar a disparidade do esqueleto apendicular de Archosauria, dedicando especial atenção ao grupo Sauropodomorpha, aplicando vários métodos numéricos e estatísticos. Concomitantemente, este trabalho visa estabelecer um enquadramento comparativo, bem como um protocolo metodológico, que permitam a inclusão de outros tetrápodes com grande versatilidade locomotora, tais como Mammalia, em morfoespaços singulares ou combinados (como Aves e Pterosauria, por exemplo).

A inclusão de estudos realizados sobre numerosos e diversos grupos, para exploração de morfoespaços de proporções em membros locomotores, é determinada pelo objectivo de criar um morfoespaço genérico de membro. Analogamente, neste contexto é importante reavaliar o conceito de padrão locomotor, complementando-o com a geração de morfoespaços empíricos de proporções.

Assente no enquadramento metodológico aqui proposto, os padrões de locomoção são a expressão de áreas de locomoção deduzidas dos morfoespaços empíricos dos dois membros - anterior e posterior. A produção deste morfoespaços possibilita a obtenção de tipos de informação distintos, mas complementares: a quantificação e a delimitação de áreas ocupadas, a variabilidade das componentes dos membros em determinado grupo, a disparidade nos diversos grupos e os intervalos de ocupação entre grupos, tudo isto a uma escala macroevolutiva. Todos estes tipos de informação foram aplicados nas diversas generalizações e formulações de hipóteses convocadas pela leitura combinada das informações sobre os dois membros.

Tendo em vista a máxima consecução dos objectivos propostos de quantificação rigorosa dos morfoespaços de proporções, os quais estão condicionados pelas características específicas inerentes ao tipo de dados em questão, foi indispensável introduzir, a partir de outras áreas científicas, métodos estatísticos tais como a Análise de Dados Composicionais (p.e., Aitchison 1986; Egozcue et al. 2003; Egozcue and Pawlowsky-Glahn 2005, 2006). A maioria destes métodos será objecto de uma introdução e descrição detalhadas no capítulo 2.

Como consequência deste enquadramento metodológico, a terminologia adoptada para descrever padrões de locomoção assenta sobre as áreas e limites do morfoespaço. Dado o carácter inovador e a originalidade da aplicação desta metodologia, as implicações dessas áreas e limites do morfoespaço num estudo evolutivo nem sempre foram cabalmente desenvolvidas. Por outras palavras, seriam

necessárias análises mais específicas e detalhadas, de modo a complementar e corroborar os sinais morfológicos apontados pelo presente trabalho. Estes estudos serão desenvolvidos em projectos futuros, incluindo, entre outros, métodos de morfometria geométrica.

2.- Como anteriormente referido, o presente estudo analisa as proporções de elementos ósseos seleccionados dos membros anterior e posterior. Ambos os membros podem ser entendidos como Supraestruturas Modulares (MS), *sensu* Rasskin (1995), estruturas organizadas através da conexão articular de elementos, que constituem unidades descritivas e mantêm uma relação de homologia clara dentro do clado Tetrapoda (Shubin and Alberch 1986; Shubin et. al. 1997). A definição de Supraestrutura Modular, no contexto desta monografia, inclui a soma de valores de comprimento seleccionados a partir de um determinado número de elementos ósseos preservados. A componente cartilaginosa da epífise nunca foi tomada em consideração, tal como não o foi o comprimento dos carpos e tarsos proximais. O estudo não inclui quaisquer elementos das cinturas pélvica ou escapular, uma vez que a incorporação desses elementos poderia originar incoerências de natureza metodológica na análise das proporções aqui seleccionadas, dado que, apesar de articulados, os membros e as cinturas constituem eixos de comparação diferentes.

Em cada Supraestrutura Modular, será examinado o *stylopodium* (úmero e fémur), um elemento do *zeugopodium* (rádio ou tíbia) e os elementos do tarso distal que fazem parte do *autopodium* (metacarpo III e metatarso III). Os critérios de selecção do elemento do zeugopodium a analisar foram sobretudo de natureza tafonómica, apesar do papel biomecanicamente relevante desempenhado pelo rádio.

As análises que se seguem centram-se no comprimento total de cada elemento dos membros. Os dados foram obtidos através da consulta de trabalhos

publicados (Dinosauria, Mammalia, Aves, Chiroptera, Pterosauria, Crocodylia) ou de observação pessoal e medição dos ossos (Prosauropoda, Sauropoda).

O objectivo é identificar e generalizar padrões de variação: em primeiro lugar, para cada elemento dos dois membros, dentro de um clado ou de um grupo estabelecido para esse efeito; em segundo lugar, para cada membro, entendido como uma Supraestrutura Modular. Este enquadramento permitiu explorar relações entre membro anterior e membro posterior, investindo particular atenção na comparação de elementos equivalentes, ou seja, comparando entre si cada componente - *stylopodium*, *zeugopodium* e *autopodium* – presente nos dois membros. Esta perspectiva metodológica possibilita a avaliação da existência (ou não) de uma tendência marcada e/ou da direcção apontada pelos padrões de variação dentro de um dos membros ou entre os dois.

3.- Os estudos das proporções dos membros têm-se tradicionalmente centrado no estabelecimento de diferenças entre padrões de locomoção e, analogamente, os estudos de disparidade sobre o esqueleto apendicular dos tetrápodes têm sido claramente influenciados por esta função. Esta perspectiva convencional, até certo ponto perfeitamente plausível, foi muitas vezes justificada por uma concepção dos membros como elementos físicos extremamente conservadores dentro da evolução específica de cada grupo, sem um sinal filogenético claramente definido. Uma perspectiva semelhante parte do princípio que a morfologia do esqueleto apendicular é condicionada pelos seus mecanismos locomotores. Estes pontos de vista fizeram com que as análises dos membros fossem escassas ou desprovidas de um maior significado no âmbito de estudos evolutivos.

Este trabalho analisa detalhadamente os aspectos que se seguem: 1) convergências locomotoras e respectiva influência nas proporções dos elementos do esqueleto apendicular – ver capítulos 3, 6 e 7, p.e. no que se refere a Pterosauria,

Aves e Chiroptera; 2) padrões de variação no seio de cada grupo analisado, de modo a caracterizar o nível de estabilidade evolutiva atingido. Será dada especial atenção a essa singularidade evolutiva que é o voo enquanto modo de locomoção e ao seu aparecimento, um fenómeno verificado apenas três vezes entre tetrápodes.

Tendo sempre em mente estes pontos de vista, raras são as análises em que a forma e as proporções são exploradas com um enfoque estritamente morfológico. Um dos principais objectos de estudo deste trabalho é a estrutura e ocupação dos morfoespaços; assim, é essencial que se centre na organização morfológica dos elementos apendiculares sob a alçada dos conceitos macroevolutivos de disparidade, integração fenotípica e modularidade (cf. p. e. Alberch et al. 1979; Maynard Smith et al. 1985; Gould 1989; Jablonski and Bottjer 1990; Erwin 1993; Zelditch and Fink 1996; Foote 1997; McGhee 1999).

A Integração Morfológica, ou a tendência dos caracteres para covariar, constitui um campo de pesquisa inaugurado por Olson e Miller, que reconheceu a sua relevância no âmbito de estudos evolutivos (1951, 1958). Os padrões de covariação são utilizados para inferir o desenvolvimento subjacente de conexões funcionais entre traços morfológicos. O trabalho original de Olson e Miller abriu caminho para desenvolvimentos posteriores, em particular o de Cheverud (p. e., 1982, 1988, 1995, 1996). Entre as ideias de Cheverud, destaca-se a postulação de que as correlações genéticas e fenotípicas estão altamente correlacionadas, o que, por sua vez, permitiu demonstrar que a estrutura da covariação fenotípica pode ser aplicada como um indicador da estrutura da covariação genética. Deve ser entendida como estreitamente relacionada com o presente trabalho a opinião de Cheverud que afirma existirem três níveis de integração morfológica: a integração funcional e de desenvolvimento, que opera numa dimensão individual; a integração genética, que opera numa dimensão populacional; e a evolução coordenada de estruturas, que opera numa dimensão evolutiva.

Dois conceitos relacionados com Integração Morfológica são os de Módulo e Modularidade. Trabalhos de Wagner (1995, 1996b) e Magwene (2001) exploram a concepção de organismo como uma composição constituída por partes semi-independentes. Estes conceitos evolutivos indicam que os traços morfológicos podem estar estreitamente relacionados em termos de ontogenia ou função.

O conceito quantitativo de disparidade foi utilizado em numerosas análises macroevolutivas, como acima referido. Este índice numérico é usado como um indicador da "mancha de ocupação ou espaçamento das formas em morfoespaços" (Eble 2005, p. 230, tradução própria) e revelador da singularidade fenotípica de uma amostra. Eble (2005) postula que a disparidade pode ser considerada uma medida geral de variação e, face a alguns problemas de evolução morfológica, este conceito pode ser interpretado como um indicador de tendências em modularidade variacional.

No presente estudo, o facto de se assumir a relação entre disparidade e modularidade é determinante em várias secções, tais como a que se dedica à exploração da disparidade do esqueleto apendicular e do tamanho absoluto – ponto 6.5 e capítulo 7.

A disparidade pode ser medida de diversas maneiras, sendo a mais comum a que se entende como "the total variance or the total range of *n* variables in a sample" (Eble 2004, p. 266). Como se pode concluir pelos procedimentos metodológicos e pelas análises efectuadas nos capítulos 2, 3, 6 e 7, esta foi a definição preferida neste trabalho.

O conceito de modularidade acarreta outros, como o de organismo enquanto níveis hierarquicamente constituídos e o de fenótipo enquanto unidades vastamente separadas nas quais a selecção dá origem a respostas biológicas distintas e relativamente independentes. A modularidade organizacional (Eble 2005), ao reflectir unidades de estabilidade – unidades organizacionais – está ligada às interacções que se consideram relevantes na formação ou actividade dos organismos. A modularidade

variacional (Eble 2005), que reflecte as dimensões das interacções e as suas potenciais interrupções, pode ser detectada a partir dos padrões de variação e covariação das unidades descritivas que, neste trabalho, são os elementos dos membros. As variáveis morfométricas do presente trabalho, ou seja, os comprimentos dos elementos dos membros e as respectivas proporções, são consideradas unidades de variação morfológica. Eble (2004) postula que os conceitos de modularidade variacional e disparidade podem estar associados, visto que "disparity can be expected to be promoted by variational modularity, because modularity allows opportunities for semi-independent variation" (p. 266).

As medidas de variação e covariação serão combinadas como um indicador numérico tanto de modularidade, como de integração morfológica, conceitos que estão, como acima referido, intimamente ligados.

Um estudo recente de Mitteroecker e Bookstein (2007) sistematiza alguns conceitos e revê diversos princípios e métodos de Integração Morfológica e de estudos sobre Modularidade. Estes autores também tendem a dissociar os conceitos de morfologia evolutiva acima mencionados.

O estudo da variação nas proporções do esqueleto apendicular de diferentes taxa assenta inicialmente no estudo da disparidade morfológica, que avalia o intervalo de variação fenotípica dos elementos em análise. A disparidade, assim definida, pode ser visualmente representada num morfoespaço constituído sobre um diagrama ternário. Neste tipo de morfoespaço, podem ser igualmente aplicados métodos estatísticos como a Análise de Dados Composicionais – ler abaixo, para avaliar a relevância estatística das áreas de morfoespaço ocupadas no que se refere aos taxa em análise. A métrica Distância de Aitchison (A.D.) traduz, por sua vez, uma posição específica, uma distância entre as entidades morfológicas e, consequentemente, uma definição formal das áreas ocupadas pelos grupos, tal como os seus limites dentro do morfoespaço.

Todos os capítulos do presente trabalho fazem uso desta metodologia. No final do estudo, é apresentado aquilo que poderia ser considerado um morfoespaço genérico das proporções, no qual as áreas ocupadas são avaliadas dentro de um âmbito macroevolutivo. Neste morfoespaço geral, as áreas não ocupadas mas potencialmente ocupáveis permitem a sua definição em termos de disparidade.

Parte-se do princípio que as análises de disparidade permitem identificar diferentes graus de dominância das proporções dos elementos dos membros, ou seja, permitem distinguir um membro em que a proporção de *stylopodium* prevalece claramente (dominado pelo *stylopodium*) de um em que é a proporção de *zeugopodium* que prevalece (dominado pelo *zeugopodium*) ou de outro em que a dominância se verifica por parte do *autopodium* (dominado pelo *autopodium*). Depois de se definirem as áreas ocupadas do morfoespaço relativamente a um determinado grupo, pode-se investigar os padrões de variação de cada elemento do membro dentro da supraestrutura definida – membro anterior, membro posterior. Esta nova análise de variação permite chegar a uma estimativa dos modelos de integração revelados por cada grupo. A integração morfológica foi quantificada através da análise de *Biplots* e *Balances* – ver capítulos 3, 6 e 7.

O tamanho – e o papel biológico que desempenha – é um dos factores mais relevantes numa análise morfológica. O intervalo entre tamanhos dentro de um clado ou entre elementos de um grupo pode ser considerável. O presente estudo avalia relações prováveis ou constrangimentos entre tamanho e os modelos de integração dos elementos dos membros. Este importante factor biológico está, por exemplo, no centro das reflexões que se desenrolam em torno do problema do gigantismo dos Sauropodomorpha – ler abaixo e ver capítulos 5, 6 e 7.

Apesar de os módulos dos membros anterior e posterior serem explorados separadamente nos morfoespaços ternários, um organismo é uma unidade mais profundamente integrada. Assim, é de esperar a existência de um padrão de variação

combinada, observável e quantificável, nas duas unidades que são os membros. Comprovar esta hipótese teria exigido um morfoespaço hexagonal (que representasse os seis elementos dos dois membros), mas as ferramentas estatísticas necessárias a tal tarefa não se encontram de momento acessíveis. Apesar deste obstáculo de natureza metodológica, o presente estudo explora a variação combinada de partes equivalentes – membro anterior vs. membro posterior ou úmero vs. fémur, por exemplo.

No que diz respeito à história evolutiva dos Sauropodomorpha, Carrano (2005, p. 223) declara que "most of the body-size increases occur early in sauropod evolution and were largely completed by the Upper Jurassic neosauropod radiation." Defende também que o referido aumento em tamanho corporal[*] ocorreu num pequeno intervalo de tempo entre os Neosauropoda, sendo os Macronaria os únicos Sauropoda que apresentam uma redução em tamanho. Por outro lado, os diplodocóides evidenciam uma intensificação desse aumento do tamanho corporal típico dos Neosauropoda.

Tomando em consideração as referidas tendências, verificou-se que ambos os extremos do clado Sauropoda revelam relações entre tamanho e proporções do membro posterior semelhantes, ou seja, as espécies mais pequenas de não-Eusauropoda e Lithostrotia apresentam uma disparidade de proporções mais elevada do que as espécies maiores dos mesmos grupos – ver ponto 6.8.

4.- Ainda que a existência de uma relação entre as proporções dos elementos dos membros e os padrões de locomoção de um organismo seja clara, esta não é absolutamente evidente, devido a outros factores biomecânicos que caracterizam e limitam as funções dos membros (p. e., o esqueleto axial e a

[*] "Not surprisingly, early sauropod evolution is characterized by a steady increase in body size from the condition seen in [basal sauropod] *Vulcanodon* and larger prosauropods to that in basal neosauropods, representing at least a doubling in size over some 40 million years…" Carrano 2005, p. 231.

musculatura a ele associada). É necessário um método referencial que permita estabelecer uma comparação rigorosa entre entidades biológicas distintas.

No capítulo 3, foi revista a análise de uma amostra de tetrápodes voadores, nomeadamente Aves, Chiroptera e Pterosauria. O mesmo conjunto de dados já havia sido estudado por outros autores dentro de um enquadramento metodológico composicional, mas sem a aplicação de quaisquer das Análises de Dados Composicionais aqui utilizadas. Esta foi a primeira vez que estas técnicas foram utilizadas neste tipo de tetrápodes voadores e com o objectivo de identificar padrões na ocupação de morfoespaços, assim como de quantificar a disparidade verificada nos membros anteriores. Os trabalhos precedentes dedicaram-se a questões semelhantes, mas sem utilizar a metodologia de análise CDA aqui proposta (Gatesy and Dial 1996; Gatesy and Middleton 1997; Middleton and Gatesy 2000; Dyke et al. 2006; Mcgowan and Dyke 2007).

A amostra inclui várias espécies de Aves (Passerines e não-Passerines), Chiroptera (Megachiroptera e Microchiroptera) e Pterosauria (Rhamphorhynchoidea e Pterodactyloidea) – ver tabela 3.10.

A análise CDA passou pelo estabelecimento e pela descrição numérica de morfoespaços para os membros anterior e posterior, pela quantificação da disparidade (Distância de Aitchison) entre e dentro dos grupos, pela identificação de *outliers* de acordo com essa disparidade e ainda pela aplicação de testes estatísticos às proporções dos elementos dos membros.

5.- O estudo da disparidade e da integração no esqueleto apendicular de Sauropodomorpha, tal como noutros grupos de arcossauros e não-arcossauros, é realizado nos capítulos 6 e 7. Os Sauropodomorpha são analisados dentro de um contexto filogenético e as espécies estudadas foram agrupadas de acordo com critérios em parte parafiléticos, ou seja, empregando uma hierarquia filogenética os

grupos singularizam os seus descendentes, nalguns casos, ou, noutros casos, excluem-nos. Por exemplo, os clados terminais de Sauropoda, como o clado Lithostrotia, constituem um grupo monofilético, enquanto o grupo Titanosauria exclui o clado hierarquicamente superior Lithostrotia, constituindo assim um grupo parafilético. Este referencial filogenético permite, muito embora se utilizem grupos parafiléticos, estabelecer comparações entre grupos parafiléticos distintos que constituem um nodo monofilético.

De um modo geral, as diferenças mais notórias verificadas nas proporções dos elementos dos membros verificaram-se em grandes clados. No capítulo 4, são justificados os critérios adoptados para estes agrupamentos. A selecção do contexto filogenético torna viável a investigação de dois dos aspectos mais interessantes na evolução de Sauropodomorpha: a condição de quadrupedismo ou bipedalismo deste clado e a formulação de hipóteses relacionadas com o gigantismo dos saurópodes. O capítulo 5 oferece uma breve introdução geral a esta importante questão biológica.

Este trabalho leva ainda a cabo, no capítulo 4, uma caracterização dos elementos dos membros analisados, tomando em linha de conta os agrupamentos escolhidos.

Ilustraram-se ainda os diferentes níveis de organização morfológica dos membros, de modo a permitir não só a análise morfológica das partes, mas também, a um nível mais elevado, das proporções dessas partes que constituem uma supraestrutura modular.

Epistemologicamente, os estudos de morfologia revelam diferentes níveis de informação. Embora a análise tradicional de formas não revele diferenças morfológicas substanciais nas partes dos membros entre as várias espécies do clado Sauropodomorpha, as análises feitas às proporções dos elementos constituintes dos membros revelaram uma realidade diferente.

Esta proposta pode ser melhor corroborada através da expansão da análise de forma às mais relevantes proporções, aplicando um estudo em Morfometria Geométrica, a 2 ou 3 dimensões. Esta combinação de diferentes níveis de informação morfológica iria permitir-nos "to efficiently assess patterns of form." (Rasskin 2003, p. 306). Embora o conceito de "Boundary Constraints" (Rasskin 2003) não tenha sido explorado neste trabalho, esta ideia é válida para o tipo de dados biológicos e composicionais nele utilizados.

Surpreendentemente, o tamanho desempenha um papel singular na interpretação de resultados desta investigação. Tradicionalmente, as proporções têm vindo a ser interpretadas como o resultado da relação entre tamanho e forma, mas nunca foram avaliadas separadamente. Os resultados apresentados nos capítulos 6 e 7 demonstram como o tamanho pode ser compreendido como uma variável independente das proporções. Assim, o factor tamanho foi removido da comparação de proporções de elementos dos membros e, depois, a disparidade observada nesses dados composicionais foi comparada com o tamanho absoluto.

6.- Nos capítulos 6 e 7, o enquadramento metodológico proposto é revisto e detalhadamente descrito, de modo a avaliar a magnitude dos resultados obtidos, que por sua vez estão ligados às questões de natureza biológica previamente mencionadas: as mudanças evolutivas na locomoção dos Sauropodomorpha e a sua relação com o tamanho.

Os resultados a que se chegou nestes capítulos podem oferecer três tipos de interpretações: a caracterização das novidades evolutivas entre clados, em termos de proporções e variação das partes do esqueleto apendicular; as convergências entre os diversos grupos analisados; a análise da forma como um factor condicionante vital nas proporções das partes do esqueleto apendicular.

As análises da disparidade revelam que os padrões de locomoção dos Sauropodomorpha anteriormente nomeados não são simples e imediatamente identificáveis mas, pelo contrário, se revestem de uma complexidade em muito superior à mera compartimentação num modelo bipartido de bipedalismo ou quadrupedismo.

No morfoespaço geral de mamíferos e arcossauros, os Sauropodomorpha localizam-se numa área identificável, definida pela dominância do úmero no membro anterior e do fémur no membro posterior. Embora a analogia entre saurópodes e elefantes seja recorrente, tanto em estudos já canonizados (Holland 1910; Bakker 1971), como noutros mais recentes (cf. p. e. Hutchinson 2008), o presente trabalho demonstra que a comparação é mais legítima tratando-se do membro posterior, do que do anterior.

No que se refere aos prossaurópodes, o cenário torna-se algo diferente e muito particular, uma vez que estes ocupam uma área extrema do morfoespaço, em especial no que diz respeito ao membro anterior, mas em caso algum o seu posicionamento é de algum modo comparável aos bípedes assumidos. A especificidade dos prossaurópodes pode caracterizar-se, no que se refere ao membro anterior, pela dominância do úmero, quando comparado ao dos saurópodes, que exibem uma dominância partilhada por *stylopodium* e *zeugopodium*.

Outro dos resultados mais intrigantes é que a distribuição dos grupos analisados dentro do morfoespaço de proporções não conserva qualquer relação com a sua organização morfológica ou biomecânica. De um modo geral, consegue-se distinguir um área nitidamente ocupada por mamíferos, que revela uma disparidade mais elevada, tal como uma área ocupada por arcossauros, mais limitada, embora com algumas zonas de sobreposição com mamíferos, permitindo a identificação, por exemplo, de distâncias mínimas entre grupos dissimilares (quanto ao membro anterior),

como os Ornithischia e os Perissodactyla, e distâncias superiores entre Ornithischia e Sauropodomorpha.

Os morfoespaços ternários, devido às suas propriedades intrínsecas, tornam possível discernir áreas detalhadas que, desse modo, determinam quantitativamente micro-espaços ocupados por determinados grupos. Grupos específicos como o dos Sauropoda poderiam deste modo caracterizar-se pelas suas proporções e, no que diz respeito a grupos com uma disparidade considerável, como o dos Perissodactyla, o significado biológico dessa dispersão oferece-se a uma análise que a relacione com a história evolutiva ou a taxonomia do grupo.

O estudo dos morfoespaços de proporções em si mesmo, apesar de ser aplicado como ferramenta para evidenciar tendências de mudança em proporções, não atinge na totalidade o grau de resolução necessário para responder a algumas questões de âmbito evolutivo, tais como quais as condicionantes morfológicas do bipedalismo ou do quadrupedismo entre clados ou mesmo a um nível macroevolutivo.

As análises de variações aqui realizadas permitem fazer uma estimativa dos modelos de integração inerentes a um grupo, sob uma perspectiva filogenética (clados) ou sob uma perspectiva adaptativa (modelos convergentes) – ver capítulos 6 e 7. Os modelos de integração incluem a identificação de tendências de variação ao longo de módulos homólogos, tais como membro anterior e posterior ou úmero e fémur. Em grande parte dedicando-se aos Sauropodomorpha, mas também a outros grupos, por exemplo outros dinossauros e mamíferos, são conduzidas avaliações do nível de variação de cada elemento ósseo no membro anterior, ou no posterior, ou da relação entre determinados ossos nos vários membros. Por exemplo, o nodo Sauropoda pode aqui ser definido como aquele, entre os Sauropodomorpha, em que o padrão de variação entre as três partes do membro posterior atinge o seu máximo. Complementarmente, os padrões de variação também revelam que o membro anterior dos Macronaria é o mais variável, se se comparar as proporções do úmero e do rádio

com o metacarpo. Tomando em consideração a variabilidade do úmero-rádio como uma novidade evolutiva no que se refere a Sauropodomorpha, seria de esperar uma correlação entre a morfologia e as proporções. Este é o tipo de questões levantadas por este estudo que poderão abrir caminho para futuras investigações.

A informação que diz respeito aos modelos de integração pode ser obtida através dos resultados de variância em *Biplots* e análise de *Balances*– ver capítulos 2, 3, 6 e 7. A metodologia dos *Balances* viabiliza, através da ilustração gráfica (dendrograma) de uma partição binária sequencial da variância, a revelação de tendências evolutivas nos elementos do esqueleto apendicular de Sauropodomorpha. Por exemplo, no grupo Sauropoda foi possível identificar uma redução na variância do úmero, quando comparado ao rádio.

Numa perspectiva adaptativa, uma análise mais detalhada da variação dos elementos do membro anterior e posterior facilita claramente a delimitação de um modelo de integração em prossaurópodes e saurópodes. Os primeiros apresentam baixa integração nos dois membros, resultante da elevada variação entre membros anteriores e posteriores, corroborada pelo elevado diferencial de variância do úmero e fémur. No que diz respeito à modularidade, poderia sugerir-se que os módulos do esqueleto apendicular são biomecanicamente independentes. Por outro lado, há módulos que são biomecanicamente dependentes, tais como os membros dos Artiodactyla, Perissodactyla, Iguandontia ou Carnívora (apenas em úmeros vs. fémur), em que há um baixo nível de variação entre os membros anterior e posterior – ver ponto 7.10, tabela 7.9 e figura 7.10.

A combinação de variações extraída das análises de *Balances* das variâncias de *Biplots* de ambos os membros constituirá o núcleo da definição de bípedes ou quadrúpedes. Um bípede poderia ser definido como um organismo em que o membro anterior está desacoplado do posterior e um quadrúpede como um organismo em que as variações de ambos os membros se encontram associadas.

O ponto de partida deste estudo foi mostrar que a integração dos membros anterior e posterior nas formas bípedes é inferior à integração nas formas quadrúpedes. Um dos objectivos a que o trabalho se propõe é o de compreender e avaliar o número de planos organizacionais entre as formas bípedes, dado que os prossaurópodes apresentam um nítido contraste com terópodes, aves, primatas antropomórficos ou cangurus. Este enquadramento criará a oportunidade de testar hipóteses funcionais ou biomecânicas que implicam outras estruturas de locomoção. É razoável supor que alguns dos resultados deste estudo poderão permitir a formulação de novas hipóteses de trabalho em que se considere o nível de integração de cada membro nas cinturas ou regiões músculo-esqueléticas que a ele estão funcionalmente associadas.

O tamanho, tal como anteriormente referido, é outra questão biologicamente relevante na história evolutiva dos Sauropodomorpha. Desempenha um papel fundamental na disparidade do esqueleto apendicular e este postulado implica que o tamanho do membro completo (anterior ou posterior) esteja de algum modo relacionado com as áreas de intervalo ocupadas nos morfoespaços.

Pode quantificar-se a disparidade (Distância de Aitchison) e relacioná-la com o tamanho absoluto do membro. Ainda assim, esta relação está condicionada pela filogenia, de tal modo que as tendências evolutivas dos Sauropodomorpha poderiam ser identificadas, apesar do facto de ser possível a ocorrência de tendências antagónicas nos membros anteriores e posteriores. No que a isto se refere, o membro anterior dos Neosauropoda revela uma relação inversa entre A.D. e tamanho, ou seja, as espécies maiores apresentam uma dispersão menor no morfoespaço do membro anterior. Uma vez que a variação no membro posterior dos Sauropoda é bastante mais elevada, não há uma tendência clara e generalizada que se possa identificar enquanto tal, embora fosse possível reconhecê-la em certos grupos. O percurso evolutivo do gigantismo nos Sauropodomorpha envolve, assim, e como se verificará no capítulo 6,

dois padrões de ocupação do morfoespaço do membro anterior dos saurópodes, que se podem distinguir deste modo: um correspondendo aos saurópodes basais (em que espécimes maiores revelam índices de disparidade mais elevados) e outro correspondendo aos saurópodes derivados (em que espécimes maiores revelam índices de disparidade inferiores). Como anteriormente referido, e tendo em vista o aprofundamento da caracterização morfológica do percurso do gigantismo no esqueleto apendicular dos Sauropoda, é necessário complementar as análises de proporções com outros tipos de estudos morfológicos, como a morfometria geométrica. A título de exemplo, o úmero dos saltasaurídeos (macronários derivados) revela características morfológicas únicas, tais como a proeminente crista deltopeitoral e os côndilos, divididos e expostos anteriormente (Wilson 2005). A par de outras particularidades morfológicas, tais como as verificadas no cúbito e o diâmetro transversal aumentado do rádio distal, é assim possível inferir que os saltassaurídeos têm uma postura do membro anterior mais flectida. As mudanças morfológicas citadas poderiam ser confrontadas com uma métrica da disparidade no morfoespaço, de modo a criar uma perspectiva claramente definida sobre a trajectória evolutiva do esqueleto apendicular deste grupo terminal.

7. – O enquadramento metodológico proposto no presente estudo abriu um número considerável de caminhos para futuras investigações: uma estimativa dos valores em falta nos registos fósseis através de CDA; a análise de condições particulares relativamente aos *outliers* identificados; a reconstrução da disparidade de espécimes juvenis; o estudo da relação entre integração morfológica e tamanho, através de *Balances* e de análises de variação.

Chapter 2 – Variation and Disparity metrics in ternary morphospaces

"Morphospaces and theoretical morphology. Vertebrates with six appendages are a biological impossibility, evidently for developmental reasons. Arthropods clearly lack such inhibitions. (Ironically, either this means that angels are arthropods or it is a biological refutation of the possibility of angels!)."

Douglas Erwin (2007), p. 59

". . . the zoologist or morphologist has been slow, where the physiologist has long been eager, to invoke the aid of the physical or mathematical sciences; and the reasons for this difference lie deep. . . Even now the zoologist has scarce begun to dream of defining in mathematical language even the simplest organic forms."

D'Arcy Wentworth Thompson

On Growth and Form Chapter I, p. 2

In this chapter, as in the next one, the practice of analyzing the morphological organization of organismal structures will be explored. One will deal first with the study of variation, and its statistical analysis, by means of metric data. Variation among elements from one or more homologous structures will shed light on the morphological organization of the parts.

The organization of sauropodomorph limb parts structure will be evaluated across taxa and within a macroevolutionary framework through the identification of patterns of morphospace change in species lineages. The methodological framework of morphospace-disparity will be used to identify patterns of morphological differentiation in the limbs of the different analyzed taxa. Simultaneously, the influence of limbs morphological constraints will be evaluated and guide the exploration for potential underlying factors.

Thus, the objective of this research has been centered in the exploration of limb proportions patterns in amniotes tetrapods, with special emphasis in Sauropodomorpha dinosaurs, according to Compositional Data Analysis (CDA) mathematical procedures and techniques (Aitchison 1982, 1986).

Fore and hind limb components will be studied in terms of the proportion of their parts; other examples will be taken into account for the sake of exemplifying the variation among elements that compound a structure. The study of proportions is a way to undertake the geometry of a form by means of the idea of relative dimension, applying the arithmetic and geometric properties of the organisms.

The study of bone components proportions essentially deals with what has been denominated compositional data, since those proportions must sum to one and, accordingly, cannot vary independently from each other. This fact implies several statistical limitations; the main one is that compositional data are subject to a constant sum constraint.

Compositional Data Analysis validates the usual interpretation of covariances and also of correlations, focusing the analysis on the relative magnitude and variations of components, rather than on their absolute values. The importance of comparing proportions within an anatomical module which provides information of how the parts are varying relatively to one another must be highlighted, as must be the statistical validity of the removal of the size factor that is provided by CDA. The removal of the size factor is of crucial importance in analyses where the main focus is on the relative variation of anatomical parts. The CDA offers a pack of statistical techniques which takes into account the relative information inherent to the data, and will thus be employed as a tool to identify and quantify variation among the proportions of bone parts.

This work aims to quantify and evaluate the morphological disparity and explore several morphospaces across different taxa. In order to achieve this objective a novel metric of disparity will be used: the Aitchison Distance (A.D.), which is the most appropriate disparity metric in bone proportions studies and allows the quantification of the disparity in compositional data and ternary morphospaces.

Although, as will be described in sections below, past studies dealing with bone parts proportions intended to quantify disparity and identify variation patterns in morphospaces, one believes they could have gained analytical depth through the systematic use of CDA, since these statistical techniques allow to remove most of the methodological harassments of working with compositional data, namely by avoiding problems induced by the constant-sum constraint.

The relative variance of parts will be measured and will thus allow identifying patterns of variation in the different components proportions.

CDA analysis enables the development of:

1) the relative variation of limb elements that will provide support for a better understanding of phenotypic integration or trait associations (sensu Olson and Miller,

1958). Integration will provide the basis for formulating hypotheses on functional, biomechanical, developmental, or phylogenetic causations. A thorough discussion will be afforded in the chapters devoted to Sauropodomorpha data as well as in the Dinosauria and Mammalia - chapters 6 and 7.

Sauropodomorph limbs disparity and morphospace occupation patterning will be taken into special account. The analyses of relative variation of limb bone proportions will be performed both at phylogenetic and functional levels. For the first purpose, that is to say, at a phylogenetic level, distinct sauropodomorph clades will be confronted in order to evaluate the existence of a disparity signal within the evolutionary history of the appendicular skeleton of Sauropodomorpha. The evaluation of a functional signal within Sauropodomorpha will be performed confronting the previous disparity and morphospace occupation results with equivalent computed results within other clades, namely other groups of dinosaurs and mammals.

2) the measure of disparity. Disparity is herein based on what has been denominated Aitchison Distance, which could be generically defined as a numerical indicator of how the individuals are separated in the limb proportions morphospaces - further details and explanations follow in next section.

Obviously, this work is based on a particular set of variables, and its value will reflect how the different tetrapods occupy the proportions morphospace and how they explore the mentioned theoretical construction.

Size

Although the scope of this work implicitly deals with the concept of biological size, the methodological nature of the analyses here performed, CDA techniques, and the specificity of the data, compositional data, allows us to dismiss the size factor without invalidating the results here obtained. Complementarily, in chapters 6 and 7,

size is a factor that will be tested on compositional data variables in order to evaluate the relationship of morphospaces disparity and size.

Corroborating the potential of CDA in studies of biological compositions, it is assumed that "CDA provides a fully multivariate framework for dealing with bone proportions data within several questions (…) and covariates on component composition and the differences between [groups of] components can be addressed. It is a more natural vehicle than allometric regression for analyzing part–part relationships as it respects the symmetry between the components being compared." (Muldowney et al. 2001, p.241 and p.249). These authors suggested that regression models can be fitted to the logratios employed by the CDA and that CDA is a more complete framework for inference than the allometric regression method (Huxley 1924), as it is based on a multivariate method, rather than on a series of univariate analyses (idem).

Although not being the main focus of this work, as stated below in detail, regression as well as bivariate correlation analyses will be performed on particular variables generated by the CDA in order to test size influence.

2.1. Disparity and Morphospaces theoretical background – proportions studies in biology, paleontology and biological anthropology

"The ability to detect morphological trends and occupation patterns within morphospace depends on using the appropriate measure(s) of disparity."

Ciampaglio et al. (2001), p.695

Morphological disparity could be defined as a measure of how fundamentally different organisms are (Raff 1996) as well as the spread or spacing of forms in morphological space (Eble 2000). Disparity could also be defined as the degree of morphological differentiation among taxa within groups (Foote 1999; Eble 2000;

Ciampaglio et al. 2001). The disparity concept was widely used at large lineage and temporal scales to quantify differences in shape (e.g., Foote 1991, 1993; Dommergues et al. 1996; Wills et al. 1996; Wagner 1997).

The study of relative proportions of anatomical structures has a long tradition in different fields of biological (e.g., Christiansen 2002 a, b), paleontological (e.g., Middleton and Gatesy 2000; Gatesy and Middleton 2006) and anthropological research (e.g. Ruff 2002; 2003). In dinosaur paleobiology the analysis of limb proportions focused primarily on the posture and locomotion of different groups. A varied set of limb lengths ratios has been used, such as: trunk to hind limb; forelimb to hind limb (in different combinations of bones, the most common being humerus, radius and metacarpal III in the fore limb and femur, tibia and metatarsal III in the hind limb); humerus to femur, among many others.

Despite a long bibliographic tradition, there are no records of the use of an adequate numerical methodology for compositional data.

2.1.1 Disparity - concept and disparity metrics

The morphological disparity and morphospace occupation are close concepts, widely used in macroevolutionary studies for different purposes (e.g., Foote, 1991, 1993, 1994, 1999; Wills et al. 1994), the most common of them being to confront those values with the diversity within lineages. But there are others, such as studies dealing with mass extinctions and the role played by these biological events. Erwin (1994), for example, suggested that extensive morphological innovation occurs after mass extinctions because of the availability of ecospace.

There are a number of ways to quantify disparity. The most widespread one is the average pairwise character dissimilarity and the total variance - sum of univariate variance (Foote 1997). Erwin (2007), in an extensive review on this subject, summarized the numerical procedures proposed by other authors on quantifying

disparity: “Ciampaglio et al. (2001) evaluated these and five additional measurements of disparity (total range, mean distance, number of unique pairwise character combinations, principal coordinate analysis volume and participation ratio) for their sensitivity to sample size, number of morphological characters, percentage of missing data and changes in morphospace occupation pattern“ (p.59).

Two aspects of the analyses of morphological disparity and morphospace patterning must be taken into account: variance and range. The variance captures the average dissimilarity among forms in morphospace; the range reflects the amount of morphospace occupied (Foote 1991). Therefore, and similarly to other authors (e.g., Van Valen 1974; Smith and Bunje 1999; Eble 2000), in this work the morphological disparity will be quantified as the total variance (sum of univariate variance) in the distinct computed proportions morphospaces and the term “disparity” will be used as being equivalent to “variance”.

The CDA techniques will compute the total variance of a certain group or clade that will be split into the partial variances corresponding to the different bone parts. The range of the morphospace will be computed by the mean intragroup A.D. - see sections below for further details and explanations.

2.1.2 Ternary diagrams and Morphospaces

The morphospace concept was initially introduced by Raup (1966) in a context of gastropod shell shape. This author proposed a mathematical model for the accretionary shell growth in mollusks. Later works (e.g., Raup 1967) allowed the formalization of a theoretical morphospace concept and evidenced that different invertebrates (bivalves, gastropods, ammonoids and brachiopods) are circumscribed to particular morphospace areas, that is to say, much of the theoretical morphospace is unoccupied by extant or fossil species. Therefore, Raup stated that morphology is somehow constrained and not all morphologies are possible.

The adequate formalization, if it is possible to use such a word in this field of macroevolutionary studies, of a theoretical morphospace, is a difficult task, but the following will be adopted: “A theoretical morphospace is an n-dimensional model in which each dimension corresponds to some aspect of possible biological variation (…)”, as defined by Maclaurin (2003, p.466). Accordingly, a theoretical morphospace is a depiction of all possible biological space whose dimensions correspond to certain biological characteristics.

Theoretical morphospace is conceptually linked to empirical morphospaces formalization - theoretical morphospaces, and, quoting Eble (1999, p.9): “represent, what is possible, or occupiable, and empirical morphospaces are renditions of what has actually been occupied” - detailed explanations in McGhee 1991; Rasskin-Gutman 1995; Arthur 1997. McGhee (1999) reexamined and systematized both types of morphospaces, proposing ways of formalizing these concepts, and suggested that theoretical morphospaces are based only on mathematical parameters, namely, with the absence of any measurement data, with the ability to specify nonexistent or nonviable forms and specified by a mathematical model in which the dimensions are “geometric or mathematical abstractions of form” (p.14).

Complementary, empirical morphospaces are based on statistical conceptions dependent on sample size, character choice, and the production of multivariate ordination spaces.

The ternary diagram offers an exploratory tool for both theoretical and empirical morphospaces constructed by the relative contribution of three elements simultaneously, and the combination of compositions of more parts, illustrating all the possible combinations theoretically possible or observable. The ternary diagram is a very intuitive tool and consists of an equilateral triangle such that a generic sample X = [perA, perB, perC], in which perA is the relative proportion of A, perB the relative proportion of B and perC the relative proportion of C. Each of the three axes

corresponds to one of the parts and it is scaled from 0 to 100% (opposite vertices). Plotting the sample X, illustrated in figure 2.1, the three parts will converge to a point in this ternary morphospace.

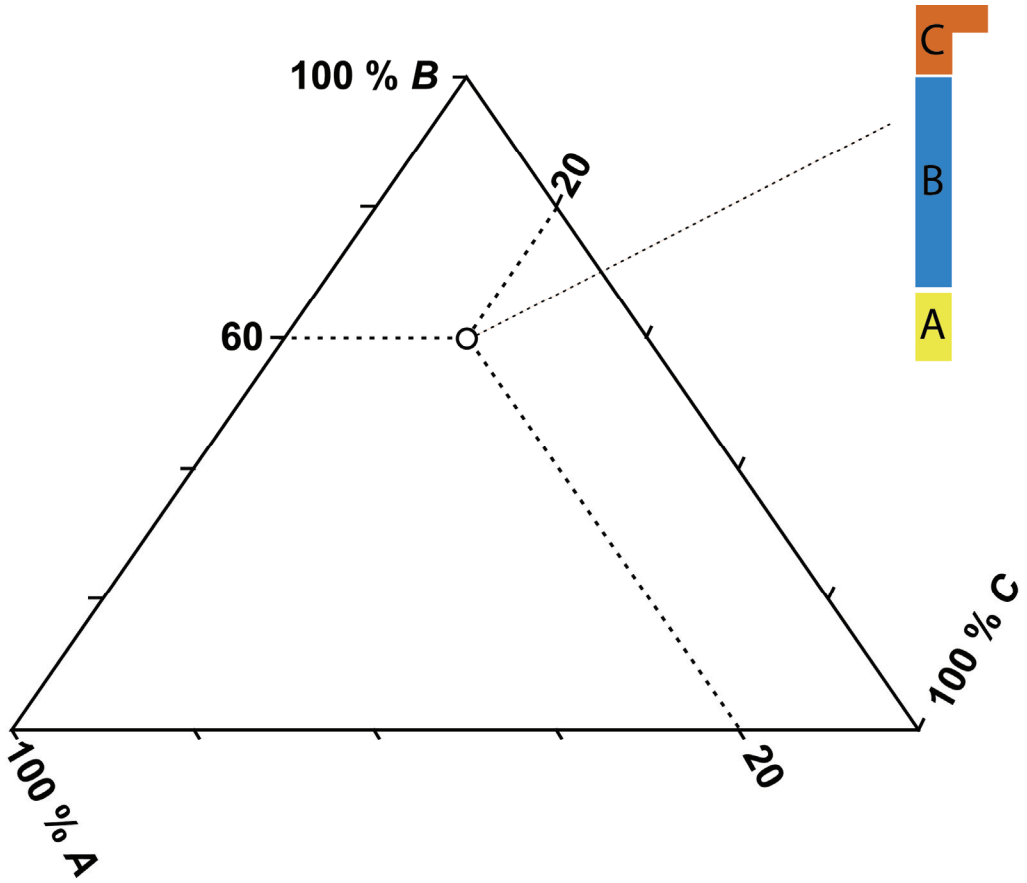

Figure 2.1 Ternary diagram of parts A, B and C and the positioning of the hypothetical specimen in the ternary diagram.

In this case, the hind limb hypothetical proportions are represented – in each axis are represented the percentages of stylopodium (femur), zeugopodium (tibia) and autopodium (metatarsal III). Each apex and each side of the triangle corresponds to impossible forms based on these limb segments, since there could not be a viable tetrapod with, for example, 0% of tibia.

Also represented are “extreme” forms here considered as elements representing more than 50% of the total limb length. If one combines the two

morphospaces, each for fore and hind limb, one could explore the forms present in this theoretical morphospace.

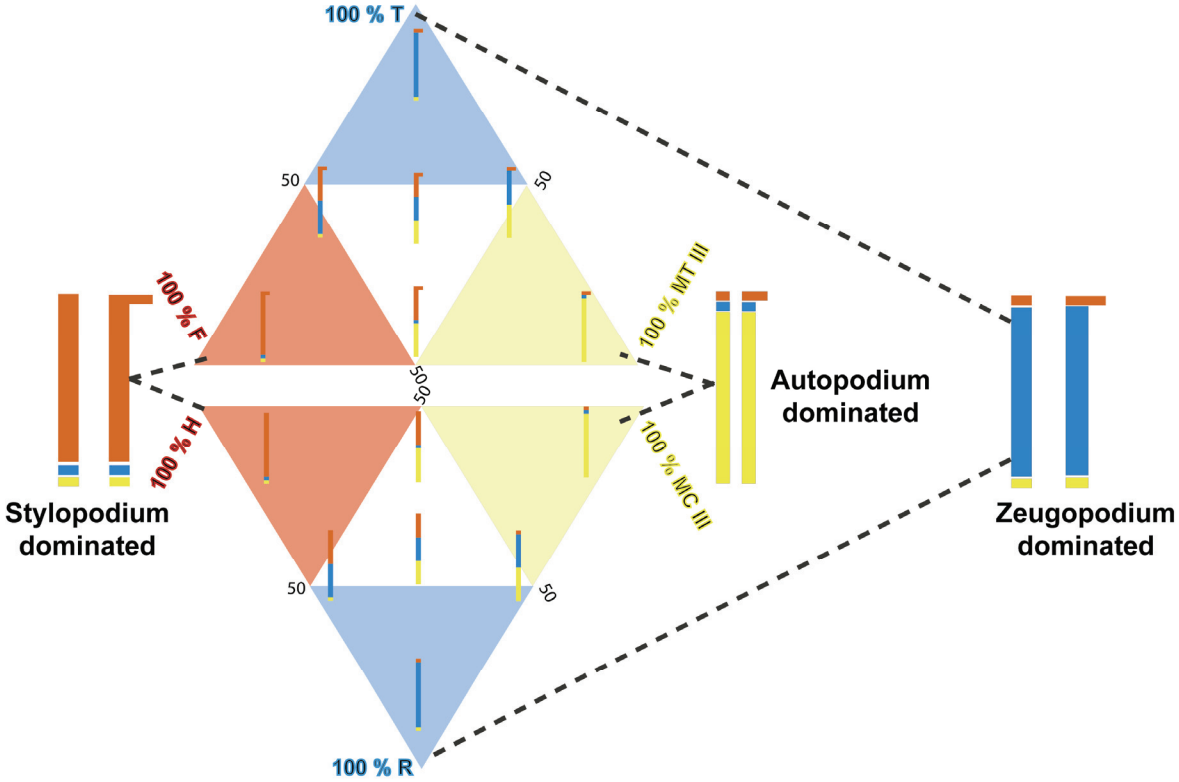

Figure 2.2 Theoretical morphospaces of both fore and hind limb proportions of 6 parts. Extreme (more than 50% of one part) limb forms morphospace areas are indicated. Abbreviations: **H** - humerus; **R/U** – radius; MCIII - metacarpal III; F - fémur; T - tíbia; MTIII - metatarsal III.

One could have extreme limb forms in which one part of the limb represents more than 50% of the total length. Therefore, one could have stylopodium-dominated limbs, in which more than 50% of the total length comes from stylopodial elements (humerus and femur). One could also have autopodium dominated limbs, in which both limbs are dominated (more than 50%) by autopodial elements (MC III and MT III). Analogously, one could have zeugopodium-dominated limbs, in which more than 50% of the total length in each limb results from the length of zeugopodium bones. Below, some of these concepts in empirical morphospaces of diverse taxa will be analyzed in detail.

These theoretical morphospaces also involves the existence of “hybrids”, extreme limb forms which are combinations of different extreme forms for each part of

the limb. For example: a “hybrid” form in which the fore limb is stylopodium dominated and the hind limb is zeugopodium dominated. The possible combinations of “hybrid” extreme limb forms morphospace areas are illustrated in figure 2.3.

The theoretical morphospaces allow, therefore, exploring very intuitively the morphospace occupation of diverse groups of animals.

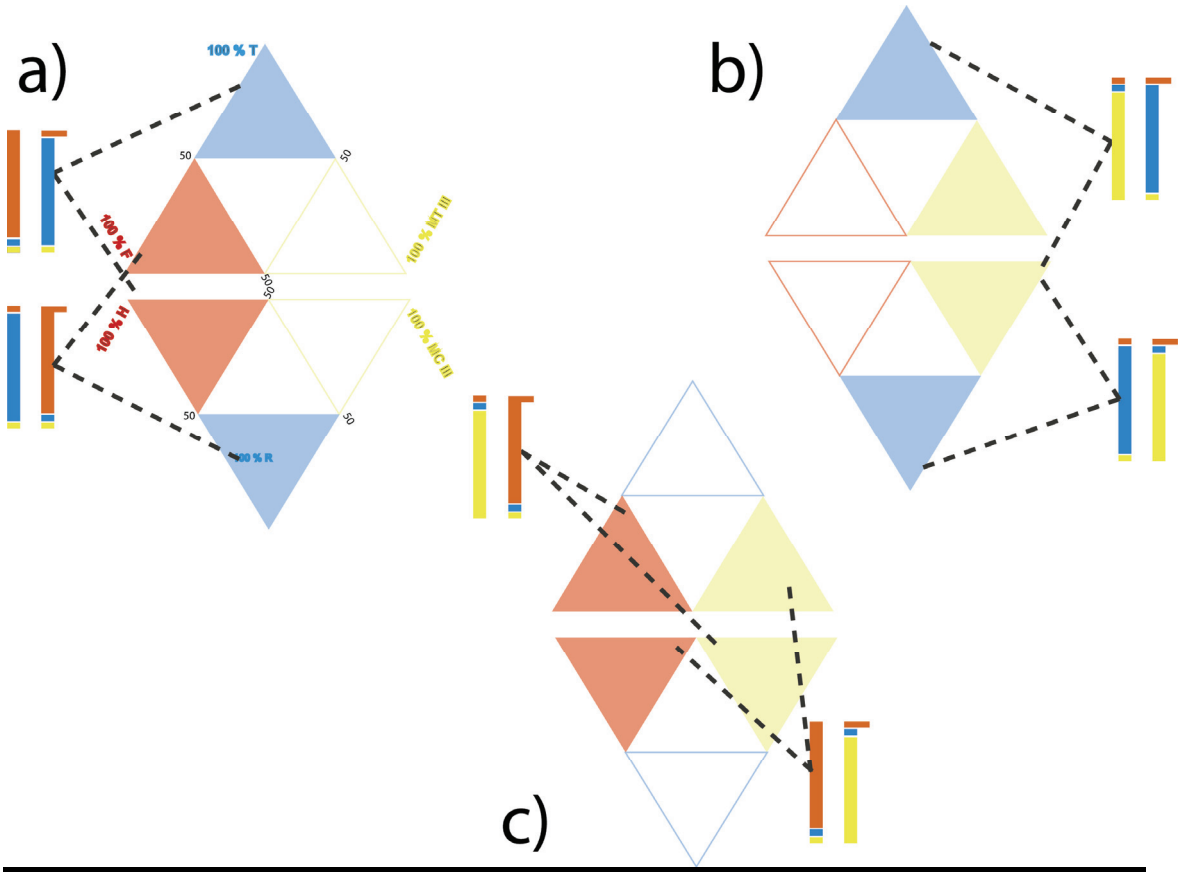

Figure 2.3 Theoretical morphospaces of both fore and hind limb proportions of 6 parts. Extreme hybrid limb forms (more than 50% of one part) morphospace areas are indicated. a) Extreme hybrid limb forms in which the limbs are dominated by stylopodium and zeugopodium elements in fore or hind limb. b) Extreme hybrid limb forms in which the limbs are dominated by stylopodium and autopodium elements in fore or hind limb. c) Extreme hybrid limb forms in which the limbs are dominated by zeugopodium and autopodium elements in fore or hind limb. Abbreviations: H - humerus; R – radius; MCIII - metacarpal III; F - femur; T - tibia; MTIII - metatarsal III.

Ternary diagrams have been used as tools for both theoretical and empirical morphospaces in a number of studies: theropod forelimb disparity and function (Gatesy and Middleton 1997; Middleton and Gatesy 2000), avian terrestrial locomotion (Christiansen and Bonde 2002), archosaur skull geometry and disparity (Marugán-Lobón and Buscalioni 2003), camelid locomotor evolution (Janis et al. 2002), pterosaur

locomotion (Clark et al. 1998), ecological polarity (Retallack 2004), Sthenurine kangaroos types of locomotion (Janis et al. 2006), turtle locomotor evolution (Joyce and Gauthier 2004), origin of primate grasping (Bloch and Boyer 2002), among many others.

Another example of a limb proportions study in paleontology is the analysis of an enormous sample of different taxa (Carrano 1998) that revealed different patterns of morphospace occupation. The analysis and quantification of morphospace occupation "were calculated as the area of an ellipse about a regression generated for each pair of variables, using range along the slope and covariance as the two axes of the ellipse" (Carrano 1998a , p. 39). Occupied areas of the morphospace are illustrated in figure 2.4.

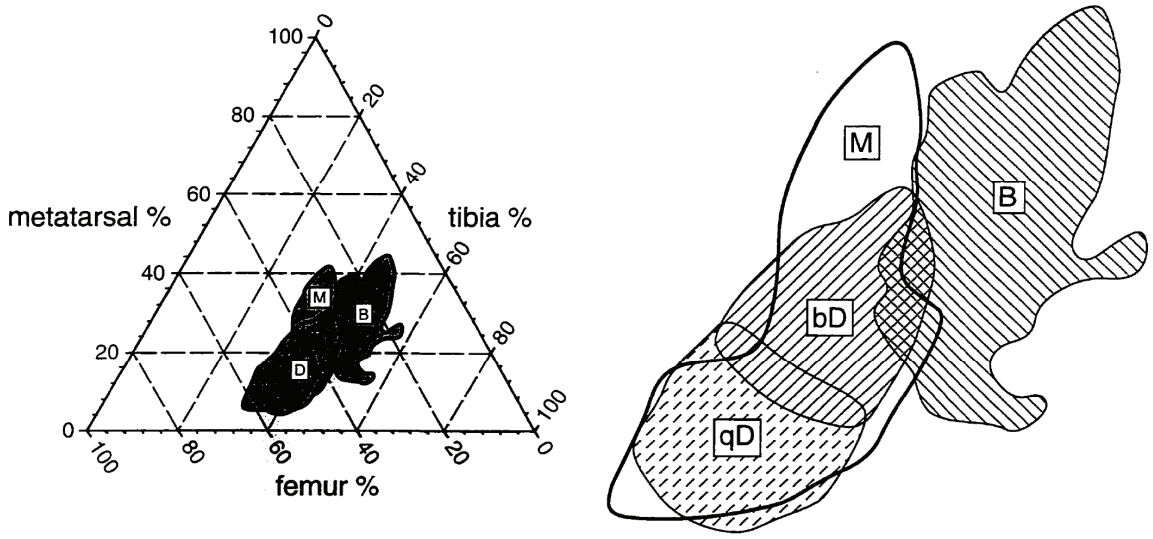

Figure 2.4 Carrano (1998) ternary diagram illustrating hind limb element proportions (femur, tibia/tibiotarsus, and metatarsus/tarsometatarsus) in mammals (M), non-avian dinosaurs (D) and birds (B). Note the areas of occupied morphospace. Adapted from Carrano (1998, fig. 2.2.).

The cited work, as well as previous ones, employed different methods of quantification of the morphospace occupation patterns and the majority of them did not identify the problematic question of the unit sum constrain, not to mention numerical inadequacies of applied methods of morphospace occupation, as discussed below.

Middleton and Gatesy (2000) and Gatesy and Middleton (2006) examined the relationship between fore limb design and function across the 230-million year record of theropod dinosaurs. Fore limb disparity was assessed by plotting the relative contributions of the three main limb elements on a ternary diagram - lengths of the humerus, radius, and metacarpal II. Since the principal purpose of the referred study was to establish a relationship between design and function, five functional groups were created.

The analyses performed on this data set concerned only the occupation patterns of limb elements in a ternary diagram. The occupation patterns were carried out visually and quantified by the "…linear distance between pairs of points. This distance, divided by the maximum possible distance between two points (from one vertex to another) yields a disparity index (DI)" (Middleton and Gatesy 2000, p. 152). Additionally, it is assumed that limbs with similar proportions will be restricted to one area of the morphospace, while more "disparate limbs will be spread out into a larger point cloud" (Gatesy and Middleton 2006, p. 276).

As it can be seen later on this work, these sorts of measures are not appropriate for this type of data, that is to say, compositional data, due mainly to its numerical intrinsic characteristics.

Different analyses of bone component proportions essentially deal with compositional data, because they are proportions that must sum to one and, accordingly, cannot vary independently from each other. This fact implies several statistical constraints; the essential one is that compositional data are subject to a constant sum constraint. This sum constraint consequently forces other constraints upon the variance -covariance matrix of X, overthrowing most standard statistical approaches - namely techniques based on regression and multivariate analysis - which rely on an assumption of multivariate normality. See below theoretical background of CDA for detailed methodological explanations and analyses.

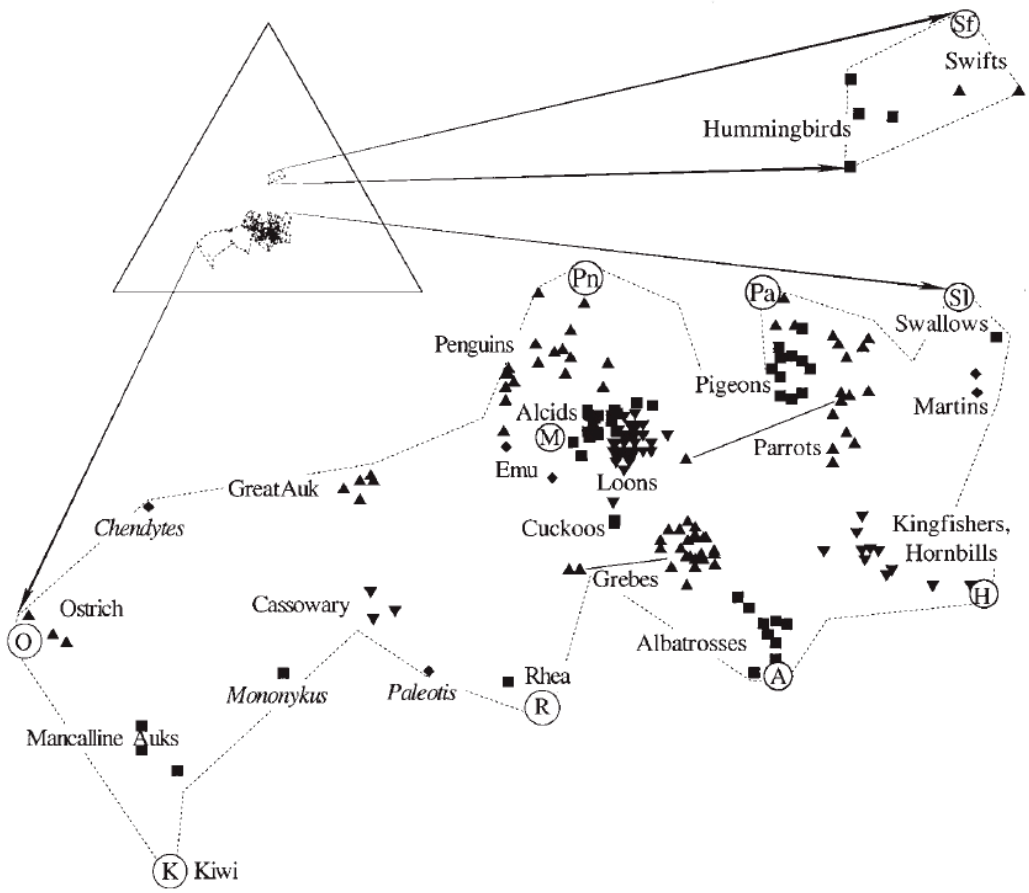

Figure 2.5 Middleton and Gatesy (2000) fore limb proportions for selected groups of birds. Adapted from Middleton and Gatesy (2000, fig. 6).

2.2 Compositional Data Analysis - theoretical background

2.2.1 Introduction

The history of compositional data starts in 1897, when Karl Pearson wrote his celebrated paper about spurious correlations into a biological context. The main idea of the paper was to state the impossibility of correctly interpreting the covariances and correlations among parts of a compositional vector. In fact, if the covariance matrix of a compositional data set is computed, it can be shown that the sum of each row is always equal to 0. This is a consequence of the constant sum constraint. One realizes

that at least one element of each row, the variance, is positive* and, consequently, it necessarily has to obtain a negative covariance. This fact invalidates the usual interpretation of covariances and also of correlations.

Since that time, a lot has been said and wrote about the statistical analysis of compositional data. Nevertheless, the solution appears in 1982, when John Aitchison proposed the use of logratios (Aitchison, 1982). Eventually, Aitchison (1997) formulated the fundamental principle of compositional data: “Any meaningful (scale invariant) function of a composition can be expressed in terms of ratios of the components of the compositions” (p. 18). Then, when one has a compositional problem, the interest lies in the relative magnitude and variations of components, rather than in their absolute values, and this is achieved working with logratios.

From that period on, the approach has seen a great expansion, and a "natural geometry" for compositions, coherent with this intuitive concept of difference between compositions, is introduced – see, for example, Aitchison et. al. (2002) or Egozcue and Pawlowsky-Glahn (2006), for an extensive review.

A Euclidean vector space structure, based on the relative scale, is also defined on the simplex, the sample space of compositional data - see Pawlowsky-Glahn and Egozcue 2001 or Billheimer et. al. 2001, as examples, in geological and biological contexts, respectively. The operations are easy but unusual. Let C(·) denote the closure operation which normalizes any vector x to a constant sum (Aitchison, 1982), and let be x; x* two D-part compositions and α be a scalar. Then, the inner sum, called perturbation, is defined as

$$\mathbf{x} \oplus \mathbf{x}^* = C(x_1 x_1^*, x_2 x_2^*, \ldots, x_D x_D^*);$$

the outer product, called *powering*, is defined as

$$\alpha \otimes \boldsymbol{x}^* = C(x_1^\alpha, x_2^\alpha, \ldots, x_D^\alpha).$$

* Except for the trivial situation of a constant component, where the variance is zero.

The perturbation operation is equivalent to translation in real space and powering is equivalent to the scalar product in real space.

There are two equivalent ways of dealing with compositional data. The first one is called “stay in the simplex” (Aitchison 1986; Pawlowsky-Glahn and Egozcue 2001) and consists in using the special geometry and the specific operations of the simplex: Perturbation, Powering and Aitchison Distance - see next section. This approach is based on the idea of working on coordinates, as working on coordinates with respect to the classical Euclidean geometry is equivalent to work on the simplex with respect to Aitchison geometry. The second way is based on working with transformed data, grounded on logratios, in order to move from the simplex to the real space and then apply all the standard statistical methodology. This "move approach" is “based on working with the simplex embedded in real space, with the usual Euclidean geometry” (Pawlowsky-Glahn, pers. commun.). The second way concerns to coordinates in real space, which are not necessarily orthogonal, e.g., the *alr* transformation.

“Staying in the simplex”

In the following sections, some of the CDA transformations, the logratios properties as well as the disparity metric used herein are going to be introduced.

2.2.2 Aitchison Distances (A.D.)

As previously described, there are several advantages of using the compositional proper transformations. These include, firstly, to remove the unit sum constrain quantitative problems in order to obtain rigorous numeric comparison among the used data.

In the analyses of compositional data morphospaces, as seen before, as well as on the identification of patterns of morphospace occupation, different units of comparison of the specimens have been used. An important element in geometry is the

distance between two elements. Its mathematical definition is always associated with the geometry defined on the sample space and in particular with the inner product. A relative squared distance, coherent with the special geometry required for any compositional data and with the Aitchison inner product (Aitchison, 1986) is

$$d_a^2(\mathbf{x},\mathbf{x}^*) = \frac{1}{D}\sum_{i<j}\left(\ln\frac{x_i}{x_j} - \ln\frac{x_i^*}{x_j^*}\right)^2 .$$

This distance is directly defined on the simplex, i.e. $\mathbf{x},\mathbf{x}^* \in S^D$, that is to say, working with the proportions or percentages, satisfying all the standard mathematical properties required, and is relative and coherent with our intuitive concept of difference. Working with A.D. distances is the proper way to calculate distances in the simplex, being equivalent to working with Euclidean distances of the transformed data (*clr* or *ilr*).

To illustrate the differences, some 3-part compositions representing proportions of braincase, orbit and rostrum, from Marugán and Buscalioni (2003), for 4 specimens labeled as A, B, C and D are plotted on the ternary diagram - figure 2.6. Specimens A and B correspond to Aves and specimens C and D to Pterosauria. From an euclidean point of view the distance between A and B is the same as between C and D (d(A,B)=d(C,D)=0.03), but if one uses the relative distance (Aitchison Distance) one finds that the distance between C and D doubles the distance between A and B (da(A,B)= 0.11, da(C,D)=0.22). This example exposes some of the quantification problems involved in ternary diagram analysis. Special care in the analysis should be taken in the areas near the vertices – see figure 2.6., representing how "apparent" equivalent distances on the ternary correspond to different distances in the real space.

Note that when any multivariate statistical analysis on compositional data is performed, it has to be coherent with this structure, that is, the key and most important aspect is to make sense in our perception of the natural scale of the data. Thus, we can work directly with our compositions using the particular geometry, or one can work

with logratios using the usual geometry of real space - see below, as well as Egozcue and Pawlowsky-Glahn (2006) for an extensive discussion.

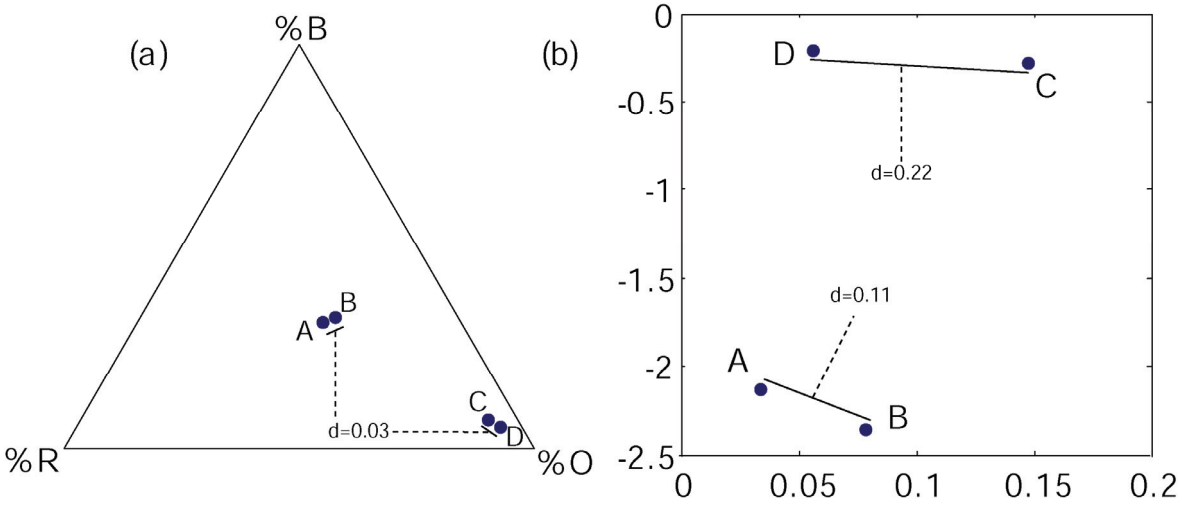

Figure 2.6 Proportions of braincase, orbit and rostrum of two birds (A: *Athene noctua*, B: *Coccothraustes vespertinus*) and two pterosaurs (C: *Pteranodon ingens* and D: *Pterodaustro guinazui*) are plotted on the **(a)** ternary diagram, where *d* represents Euclidean distance and **(b)** the corresponding logratios on the real space, where *d* represents Euclidean distance, equivalent to the A.D. on the Simplex, as stated above.

2.2.3 Centering

The center of a compositional data set X of size n is g, the closed geometric mean, which is formally defined as

$$g = C[g_1, g_2, ..., g_D], \text{ with } g_i = \left(\prod_{j=1}^{n} x_{ij}\right)^{1/n}, i = 1,2,...,D,$$

which is a measure of central tendency for compositional data and, again, consists in the closed geometric mean (Aitchison 1997).

Once the centre of a compositional data set is defined, one could carry out the centering operation, i.e., the routine that returns the data set $X^* = (g)^{-1} \oplus X$. Thus, the centering transformation, first introduced by Martín-Fernández et al. (1999), is a perturbation† that serves to move our data set into the center of the simplex, that is, the center of the perturbed data set is now e, the barycenter of the simplex. An

† For definition of Perturbation see 2.2.1.

extensive discussion of the centering transformation can be found in von Eynatten et al. (2002), where it is shown that a perturbation transforms straight lines into straight lines, that is to say, gridlines and compositional fields can be incorporated into the graphical representation without the danger of a nonlinear distortion.

In order to demonstrate this special geometry, a theoretical example is illustrated in figure 2.7. In this case, two simulated groups of 3-part compositions were generated. One is near the center of the ternary diagram (group 1), while the second is near a vertex (group 2). If one observes these two sets using the incorrect Euclidean point of view, it could be concluded that one group is approximately the translation of the other. This remark is not true if one takes into account the natural geometry for compositions. In fact, if both data sets are centered, one can clearly see that the distances between elements in the second group are higher from those obtained in the first group.

Therefore, the centering transformation is particularly important and should be taken into special account when one has any biological composition with one or more parts close to the apices of the morphospace.

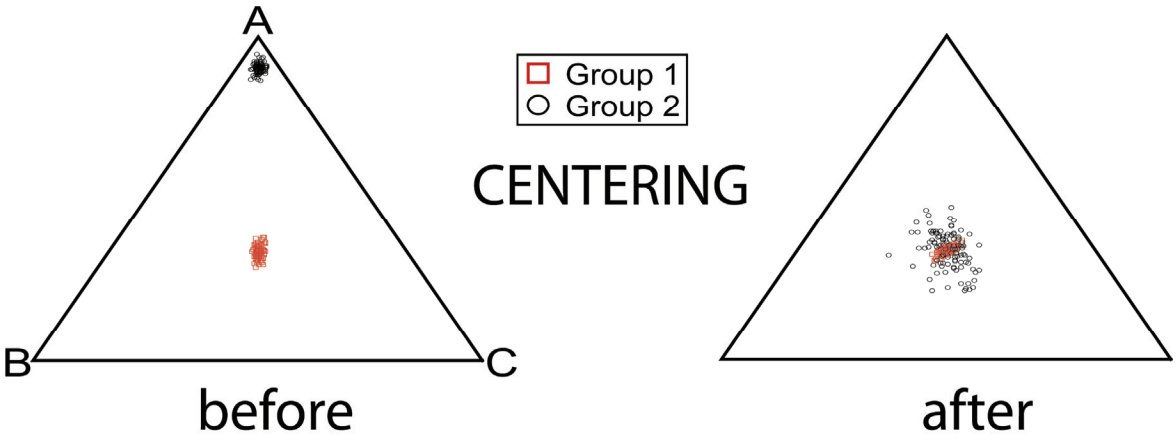

Figure 2.7 Dispersion patterns in two distinct areas of the ternary diagram, before and after centering. Note that the dissemination pattern in areas near apex – group 2 – increases its dissemination pattern after centering. Group 1, located in the central area of the ternary diagram preserves similar distribution pattern. 200 specimens aleatory generated: Group 1 generated with Normal mean part A=33.3%, B=33.3%, C=33.3%, variances part A=0.02, B=0.02, C=0.02; Group 2 generated with Normal mean part A=90.5%, B=4.75%, C=4.75%, variances part A=1, B=1, C=1. Note that the centering has been done independently for each group.

"Moving to the real space"

2.2.4 Logratio Transformations

There are distinct logratio transformations, but the present chapter introduces only two of them, which are also applied in chapters 3, 6 and 7: the Centered Logratio Transformation (*clr*) and the Isometric Logratio Transformation (*ilr*).

Given a D-part composition x, the *clr* is given by

$$y = clr(x) = \ln \frac{x}{g_D(x)},$$

where $y \in \Re^D$ and $g_D(x)$ is the geometric mean $\left(\prod_{i=1}^{D} x_i\right)^{\frac{1}{D}} = \exp\left[\frac{1}{D}\sum_{i=1}^{D} \ln x_i\right]$ of *D* components of x (Aitchison 1986). This operation transforms the data from their constrained sample space, the simplex, into the real space‡. The *clr* is symmetric in the parts and is also an isometric transformation.

Consequently, and once again, the data can then be analyzed after the specific transformations by most of the traditional multivariate analysis tools not relying on a full rank of the covariance (Aitchison 1986).

The *clr* covariance matrix possesses all the statistically desirable property of symmetry of all D-parts. Reyment and Jöreskog (1993) stated that "The centered logratio covariance matrix (…) is the most suitable point of departure for constrained principal component analysis. The usual method of extraction of eigenvalues and eigenvectors is used." (p. 126). Nevertheless, the covariance matrix of the *clr* data is singular.

In order to solve the problem of the singularity of the *clr*-covariance matrix Egozcue et al. (2003) introduced the *ilr* transformation. Although the *clr* transformation

‡ In fact into a subspace of the real space, namely an hyperplane which goes through the origin, as the transformed vectors must sum to zero. (Pawlowsky-Glahn pers. commu.)

is unique, there are infinite numbers of *ilr* transformations. Given a D-part composition x, the first *ilr* defined is given by

$y = ilr(x)$, where $y_i = \frac{1}{\sqrt{i(i+1)}} \ln\left(\frac{x_1 x_2 \cdots x_i}{(x_{i+1})^i}\right), i = 1 \ldots D-1$ and $y \in \Re^{D-1}$

This operation transforms the data from their constrained sample space, the simplex, into the real space. The *ilr* is an isometric transformation, although its interpretation is not straightforward for non-specialists. In order to minimize this difficulty, a specific kind of *ilr* transformation, called balances, will be introduced in section 2.2.6.

Performing the *ilr* transformation, one can apply all multivariate statistical methodologies.

2.2.5 Variation matrix, total variance and *clr*-variances

There are several ways to describe the relative variability of a compositional data (Aitchison 1986). In this section only the ones used in this work are described:

- the variation array contains, above the diagonal, the variances of simple logratios, whereas, below the diagonal, the means of simple logratios are represented.

$$\begin{pmatrix} - & \mathrm{var}\left[\ln\frac{X_1}{X_2}\right] & \cdots & \mathrm{var}\left[\ln\frac{X_1}{X_D}\right] \\ E\left[\ln\frac{X_1}{X_2}\right] & - & \ddots & \\ \vdots & \ddots & - & \mathrm{var}\left[\ln\frac{X_{D-1}}{X_D}\right] \\ E\left[\ln\frac{X_1}{X_D}\right] & \cdots & E\left[\ln\frac{X_{D-1}}{X_D}\right] & - \end{pmatrix}$$

- total variance is a measure of variability of the whole data set and consists on the sum of all elements above the diagonal of the variation array divided by the number of parts of the composition.

Finally, given a *clr* transformed data set it is possible to compute its covariance matrix. Its diagonal contains the variance of the *clr* transformed parts. Each element is known as *clr*-variance. Also, the sum of all *clr*-variances is equal to the total

variance. Last, the total variance could also be calculated as the sum of the *ilr* variances.

2.2.6 Isometric log ratio (*ilr*) and Balances dendrograms

Balances is a specific kind of *ilr* coordinates associated with groups of parts (Egozcue and Pawlowsky-Glahn 2005) and simultaneously an intuitive way of exploring compositional data. In other terms, balances are "the coordinates which represent an element of the simplex in the orthonormal basis defined by a sequential binary partition." (Egozcue and Pawlowsky-Glahn 2006, p.13).

Projected samples are summarized in a dendrogram-like graph showing:

a) the way of grouping parts;

b) the explanatory role of sub-compositions generated in the partitioning process;

c) the decomposition of the variance;

d) the centre and quantiles of each balance.

The detailed mathematical description of this methodology is far beyond the scope of the present work. Instead, the fundamental equations of this methodology (Egozcue and Pawlowsky-Glahn 2005; Egozcue et al. 2003; Pawlowsky-Glahn and Egozcue 2005), as well as the description of the fundamentals of data analysis used in this part of the work, will be introduced.

The balance-, for the i-th order of the partition, is $b_i = \sqrt{\frac{r_i \cdot s_i}{r_i + s_i}} \ln \frac{(\prod_{x_j \in G_{i1}} x_j)^{1/r_i}}{(\prod_{x_l \in G_{i2}} x_l)^{1/s_i}}$,

where r_i is the number of parts of the numerator, i.e., in group Gi1, and s_i is the number of the parts in the denominator, i.e., in group Gi2.

The sum of the variances of all balances is also the total variance, i.e., the total variance goes through an additive decomposition of the various balances, each with a variance associated.

If one wants to examine the variation among a composition of six parts, in this work being the bones of fore and hind limb of the animal, and depending on the specific objective of the study, one will choose the adequate combination of balances. In this example one starts with the balance which compares the fore and the hind limb proportions followed by other balances explained in table 2.1.

Balance	BONE						Anatomical/Analytical meaning
	H	R	MC	F	T	MT	
B1	1	1	1	-1	-1	-1	fore limb vs. hind limb
B2	1	1	-1	0	0	0	humerus and radius vs. metacarpal
B3	1	-1	0	0	0	0	humerus vs. radius
B4	0	0	0	1	1	-1	femur and tibia vs. metatarsal
B5	0	0	0	1	-1	0	femur vs. tibia

Table 2.1 Sequential binary partition (SBP) used in the balance analysis illustrated in figure 2.8.

According to table 2.1, the balances will be computed for each sample as follows:

$$B1 = \sqrt{\frac{3 \cdot 3}{3+3}} \ln \frac{(H \cdot R \cdot MC)^{1/3}}{(F \cdot T \cdot MT)^{1/3}}, \quad B2 = \sqrt{\frac{2 \cdot 1}{2+1}} \ln \frac{(H \cdot R)^{1/2}}{(MC)^{1/1}}, \quad B3 = \sqrt{\frac{1.1}{1+1}} \ln \frac{(H)^{1/1}}{(R)^{1/1}},$$

$$B4 = \sqrt{\frac{2.1}{2+1}} \ln \frac{(F \cdot T)^{1/2}}{(MT)^{1/1}}, \quad B5 = \sqrt{\frac{1 \cdot 1}{1+1}} \ln \frac{(F)^{1/1}}{(T)^{1/1}}$$

In order to offer a better understanding of the methodology involved in balances, an example that is going to be analyzed in detail in the next chapter will now be briefly reported.

Figure 2.8 represents a balance dendrogram. For each group and balance there is a vertical segment which represents the associated variability within that group. The length of that segment corresponds to the variance of that balance, that is to say, a shorter segment implies that the balance has a small variance and explains a small amount of the total variance. Accordingly, a longer segment means a larger balance variance, which explains a large amount of the total variance - table 2.2 systematizes the corresponding variances.

The total variance in group A is mostly explained by B1 (fore vs. hind limb), while for group B most of the variance is explained, equivalently, by balances B1 and B4 (femur and tibia vs metatarsal III). In group D the balance that displays the most variance is B4, followed by B2 (humerus and radius vs. metacarpal III). This means that, for group D, the balance for the stylopodium and zeugopodium vs. the autopodium for both limbs explains most of the variance.

The sum of all segments (for all balances) of a group indicates the total variance of that group. In the same figure one observes that in balance B1 the group that exhibits most variance is group A, followed by groups D, B and C, in that order. This means that group A shows a larger variability between individuals, closely followed by group D, while group C is the most compact of the four. Group B has a middle position between them.

In balance B2 group A presents the second largest variance, preceded by the variance of group D and followed by minor variances in groups C and B, respectively. This means that the relative proportion of humerus and radius versus metacarpal III has little variability within the group of individuals conforming group B, while the individuals in group D show a larger variability. In other terms, in group B the image of the three parts (humerus, radius, metacarpal III) is very similar from one individual to another, independently of size, which is clearly not the case in group D.

Balance	Plateo. + Saurop.	non-Neos. + non-Eus.	Diplod.	B.T. + B.M. + Litho.	Total variance (by balance)
var B1	.0434	.0178	.0008	.0128	**.0748**
var B2	.0154	.0037	.0105	.0181	**.0477**
var B3	.0059	.0068	.0041	.0029	**.0197**
var B4	.0061	.0186	.0083	.0198	**.0528**
var B5	.0044	.0027	.0082	.0064	**.0217**
					Total variance .2167

Table 2.2 Variance decomposition for each group and respective balances. Abbreviations: B.M. – basal Macronaria; B.T. – basal Titanosauria; Diplod. – Diplodocoidea; Litho. - Lithostrotia; non-Eus. – non-Eusauropoda; non-Neos. – non-Neosauropoda; Plateo. – Plateosauria; Saurop. – Sauropodiformes.

Another important informational aspect of the balance dendrogram is the position of the segment corresponding to the variance of a group in a balance. That position corresponds to the mean of the balance or sample centre.

In B1 the center-point corresponding to group A is located closer to the right limit, i.e., closer to the parts F, T and MT. This implies that the geometric mean of those parts is greater than the geometric mean of the parts H, R and MC. Alternatively, the B1 center-point for group D is located precisely at the B1 centre, meaning that the overall geometric means of the parts of the fore limb and the parts of the hind limb are equivalent.

Observing figure 2.8 one becomes aware that the mean for B1 and B4 in group A is clearly separated from the other groups. These balances could be used as a starting point to infer a clear separation of group A from the rest. A detailed analysis of this data sub-set will be performed in chapter 6.

The procedures for the graphical representation and interpretation of balances dendrograms can be found in detail in Thió-Henestrosa et al. (2008).

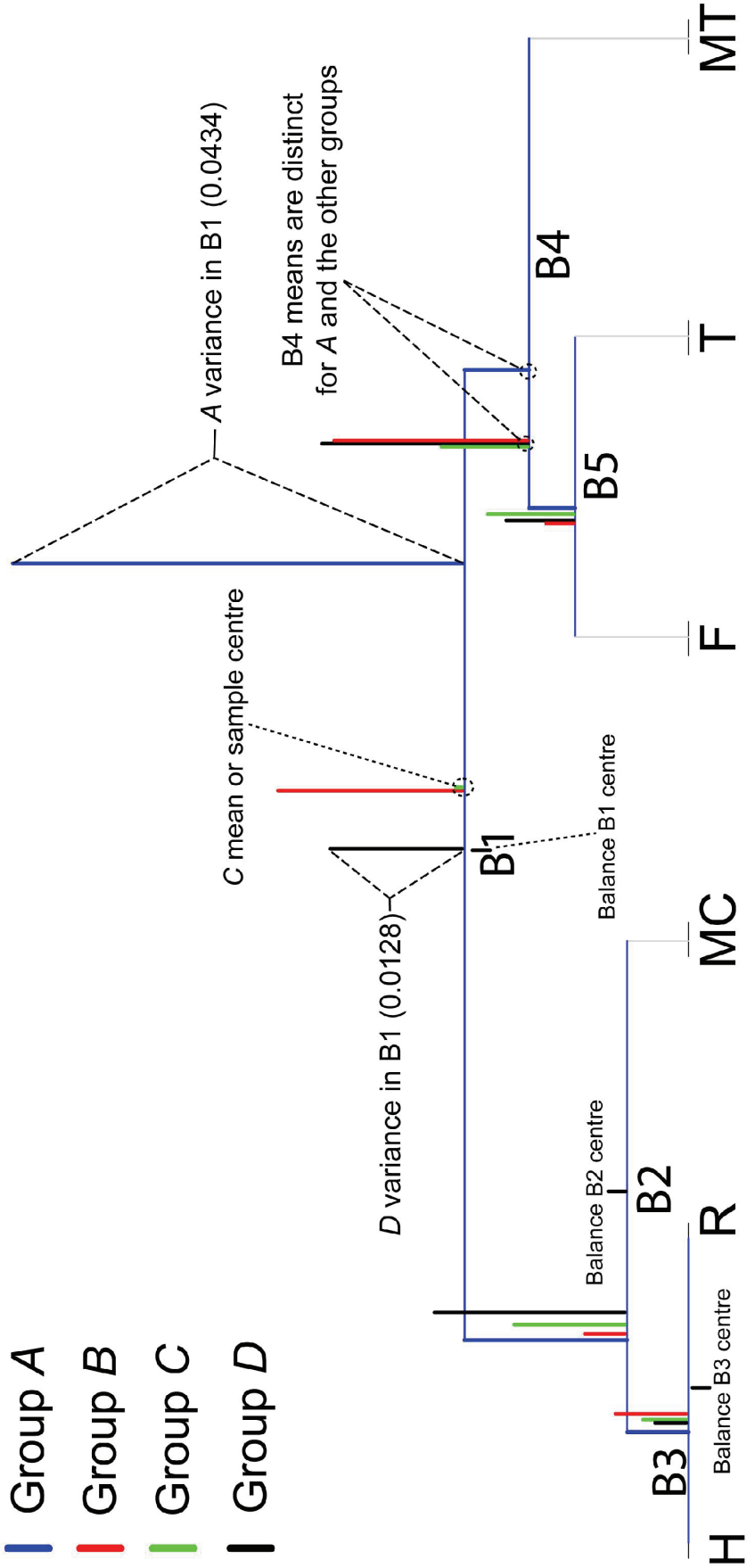

Figure 2.8 Balances dendrogram of the Sequential binary partition indicated in table 2.1 limb elements of groups variance decomposition values indicated in table 2.2. Scale (0-1).

2.2.7 Biplots

The biplots (BP) were introduced by Gabriel (1971) to represent simultaneously the rows and columns of any matrix by means of two-rank approximation. Aitchison (1990, 1997) and Aitchison and Greenacre (2002) applied the biplot to compositional data using the *clr* transformed data, that is to say, the denominator of the ratios is given by the geometric mean of each composition.

Biplot graphically describes the pattern of relative variation of a multivariate data set by projection onto a plane fixed by principal components (PC). The PC uses the *clr*-covariance matrix and the biplot is generated usually on the first two vectors, these vectors being the axes.

One of the rewards of biplot is the graphical representation of both samples and variables, here designated as cases and vertices, respectively.

The interpretation of BP requires some forethoughts which are very clearly systematized by Eynatten et al. (2003) and Daunis i Estadella et al. (2006) and can be resumed as follows:

I - The squared distance between a vertex (variable) and the origin corresponds to the variance of the *clr* transformed variable, i.e., var $\left[clr(\mathrm{X_j})\right]$. The larger the distance of the vertex to the origin, the stronger is the influence of that *clr*-variable. If the angle between the line from a vertex to the origin and an axis is small, the variable has a strong influence on the corresponding principal component.

For example: in figures 2.9. a and b, relative to prosauropod and sauropod hind limb proportions sample, metatarsal III logcentered variable exhibits the highest relative variability of all logcentered limb variables, both in prosauropods and sauropods, although they are slightly more important in the latter sample. This means that *clr*- metatarsal III strongly determines the first principal component in both sub-

samples, since the length of the vertex is approximately proportional to the variance of the corresponding *clr*-variable.

The small angle between the vertex *clr*-metatarsal III and PC1 also implies stronger influence of that vertex on the referred principal component. Comparing the two biplots depicted in figure 2.9, one sees that the relative influence of the femur on the total variability is stronger in prosauropods than in sauropods, since the vertex is longer in prosauropods sub-sample; one also detects that the relative influence of the tibia on PC2 is bigger in prosauropods than in sauropods, since the angle between that vertex and the PC2 is smaller in the former sample than in the latter.

Complete sample integrating fore and hind limb proportions

Figure 2.10 a is a biplot of the first two principal components of six limb bone elements of different groups of vertebrates based on the Dyke et al. (2006) database, which will be subjected to further detail in the next chapter. After applying CDA analyses, it can be observed that the autopodium (metacarpal and metatarsal) logcentered variables strongly influence the most important axis of variability (PC1=87%) and that the second principal component (PC2=7%) is determined mainly by the stylopodium variables - logcentred humerus and femur.

One also detects that the autopodium rays are almost orthogonal to the stylopodium rays and, therefore, an indication that the ratio metacarpal-metatarsal is independent of the ratio humerus-femur, that is to say, the sub-composition metacarpal-metatarsal and humerus-femur are independent. It should also be mentioned that fore and hind limb homologous parts are less influential on the total variability following a distal-proximal path.

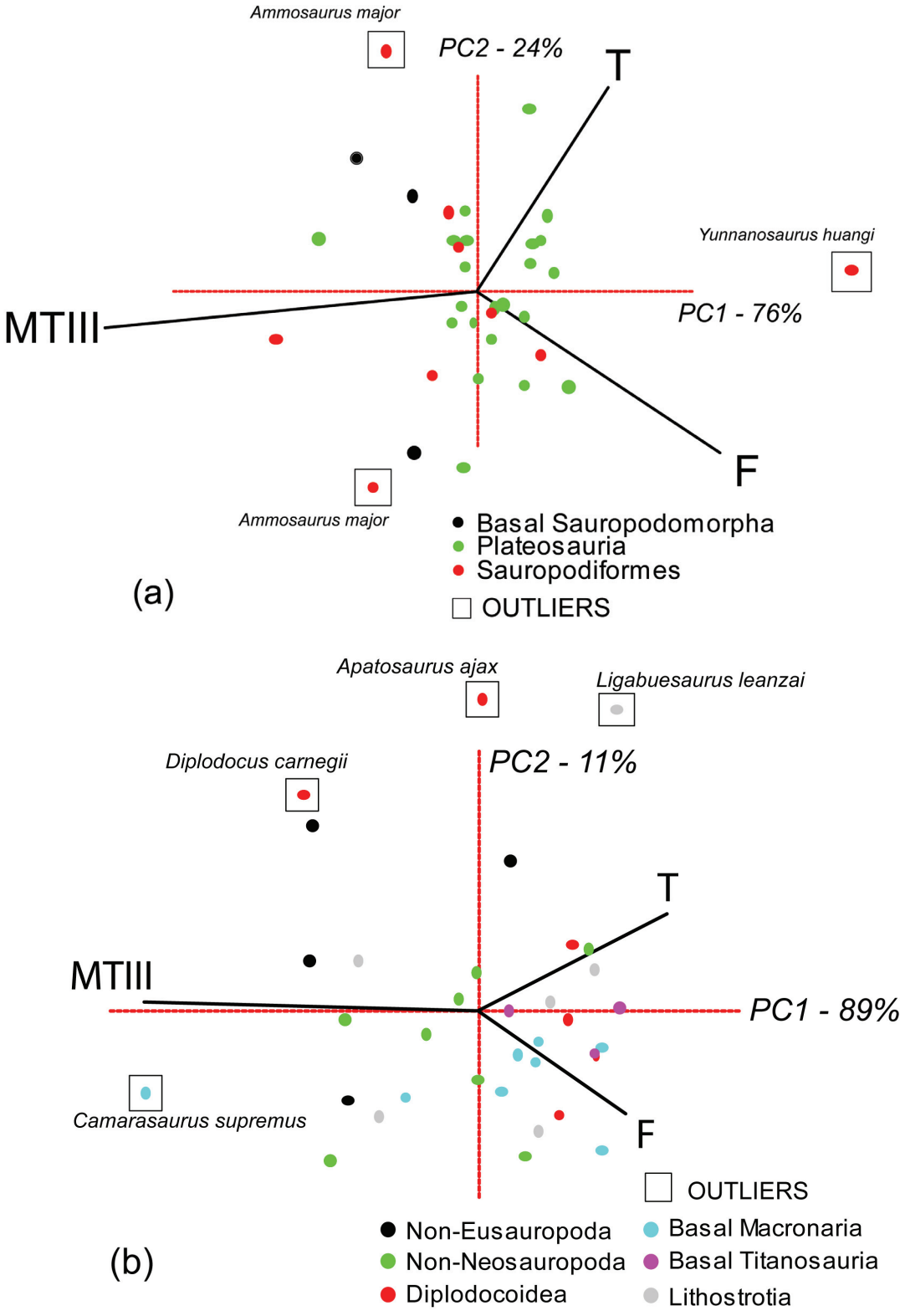

Figure 2.9 a) Biplot of the *clr*-transformed of Prosauropoda hind limb elements – Biplot of the *clr*-transformed space – First Principal Component (76%), Second Principal Component (24%). Femur (F), tibia (T) and metatarsal III (MTIII). Outliers - *Ammosaurus major* and *Yunnanosaurus huangi*. b) Biplot of the *clr*-transformed space Sauropoda hind limb elements — First Principal Component (89%), Second Principal Component (11%). (F) - femur, (T) - tibia and (MTIII) - metatarsal III. Outliers - *Diplodocus carnegii*, *Apatosaurus ajax*, *Camarasaurus supremus* and *Ligabuesaurus leanzai*.

Pterosauria

A biplot of a sub-sample of the one depicted in figure 2.10. a is represented on 2.10 b and refers to the relative proportions of six bones of fore and hind limbs of two groups of pterosaurs. The axis which explains most of the variability (PC1=61%) is influenced mainly by tibia, femur, metacarpal and by metatarsal. Comparing the two biplots one observes that *clr*-metacarpal still is the most influential factor on the total variability but *clr*-tibia turns to be an important factor in pterosaurs although the influence of metacarpal and metatarsal is also detectable as well on PC2.

Logcentred autopodium elements are, as described, an influent variability factor both in PC1 and PC2, i.e., the greatest relative variation in the ratios of components is between the two autopodial elements. The distance between the *clr*-tibia and the *clr*-femur rays is very small, that is to say, the angles between them are small and these two variables are almost collinear with the *clr*-metatarsal. This reveals a possible presence of a pattern of the subcomposition tibia, femur and metatarsal.

Observing the biplot one perceives the big dispersion of the specimens of both groups but it can be distinguished that Pterodactyloidea individuals are dispersed along the PC2, which is conditioned by stylopodium and zeugopodium parts. Alternatively, Rhamphorhynchoidea, although less clearly, are spread along the PC1, which is conditioned mainly by autopodium parts.

Another interesting fact is that hind limb bones (femur, tibia and metatarsal) proportions are practically collinear which implies that these bones exhibit a one-dimensional variability, that is to say, if one represents these three parts of pterosaurs hind limb on a ternary diagram they will be plotted along a compositional line[§].

[§] "A compositional line in S^D, containing a composition or starting point x_0 and with direction given by the composition **v**, is defined as the compositions x(t) satisfying

$$\mathbf{x}(t) = \mathbf{x}_0 \oplus (t \odot \mathbf{v})$$

for any real parameter." (Egozcue and Pawlowsky-Glahn 2006, p.149).

More detailed biplot analyses of these groups will be performed later in the next chapter.

II - The squared distance between two vertices (variables) represents the variance of the logratios of these vertices, i.e., var$\left[\ln(X_i/X_j)\right]$and that the variance of the logratios of nearly coincident vertices is near zero and, thus, the ratio is almost constant. Example: recall figure 2.10 b in which is observable that pterosaurs femur and tibia, despite having different lengths, are close together and well separated from the other variables. Those two variables have logratios variance close to zero implying that the ratio is nearly constant.

In this case one has, approximately, a ratio between femur and tibia of 0.9467[**].

III - The distance between two cases (samples) is a measure of the similarity of the two samples in composition.

IV - There is an approximate one dimensional variability of the parts metatarsal, metacarpal and tibia, which could be easily visualized in a ternary diagram with the mentioned three parts in each apex - figure 2.10 a.

V - there is a potential independence of the subcomposition humerus/femur from metacarpal/metatarsal - figure 2.10 a.

Final Remarks

Along this chapter one has generally introduced the CDA methodological protocol that was followed in the present analyzes. It will be respected, as much as possible, the referred methodology here introduced in order for the reader to establish parallelisms which allow a better understanding of the results obtained.

In some sections or chapters, namely on the reanalysis parts, the complete protocol is only partially fulfilled since not all mathematical procedures are required.

[**] That was obtained from the estimate for the E($\log(x_{femur}/x_{tibia})$)= -0.05479 in the variation array.

For each method/analysis one will discuss the biological implications of the results obtained.

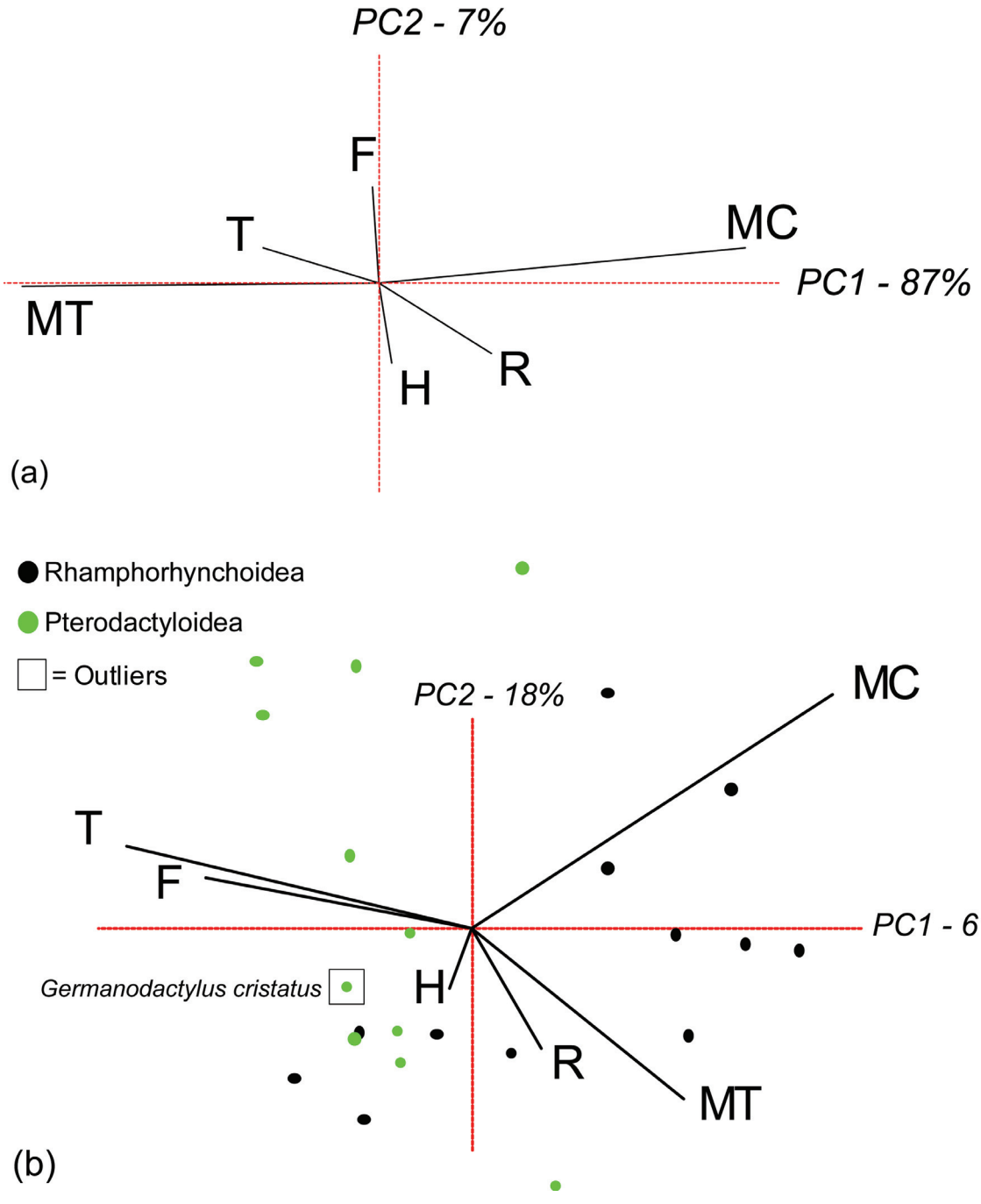

Figure 2.10 a) Biplot of the *clr*-transformed space of the first two principal components (PC1 vs PC2) of Aves (Passerines and Non-Passerines), Chiroptera, Pterosauria (*Rhamphorhynchoidea* and *Pterodactyloidea*) and Theropoda six limb parts (Dyke et al. 2006 database; see 3.2. for details). First Principal Component (87%), Second Principal Component (7%), Third Principal Component (4%), Fourth Principal Component (1%), Fifth Principal Component (1%). b) Biplot of the *clr* -transformed space of the first two principal components (PC1 vs PC2) of two groups of pterosaurs (sub-sample of 2.10 a). First Principal Component (61%), Second Principal Component (18%), Third Principal Component (14%), Fourth Principal Component (5%), Fifth Principal Component (2%). Outliers - *Germanodactylus cristatus*. Abbreviations: H – humerus; R – radius; MC - metacarpal III/IV; F – femur; T – tibia; MT – metatarsal III.

Chapter 3 - Studies under Compositional Data Analysis – examples and re-analyses

“You cannot fly like an eagle with the wings of a wren.”

William Henry Hudson

In this section some biological proportions studies that used non-Compositional Data Analysis (CDA) techniques were reassessed. The taxa here reanalyzed were studied by the original authors for a variety of objectives and purposes.

One of these works main objectives is to apply CDA techniques in order to compare the original works with the results derived from those statistical methods in order to verify the rigorous and adequate dimension of the CDA methodology.

The same methodological steps of the previous works will be followed, but in some cases, especially in section 3.2, this chapter will attempt to go beyond the work of the original authors and offer a broader limb proportions analysis.

3.1. "Disparity and geometry of the skull in Archosauria (Reptilia: Diapsida)" Marugán and Buscalioni (2003)

Marugán and Buscalioni (2003) focused on some macroevolutionary aspects of skull proportions and intended to demonstrate the existence of pattern(s) of skull proportions among a sample of Archosauria. The authors recognized the existence of a geometrical association between rostrum and braincase proportions which is integrated into a broader archosaurian skull geometry, following "a constant constructional morphological organization, where three integrated modules follow a variation rule." (Marugán and Buscalioni 2003, p.81).

Although recognizing the innovative quality of this work, herein it is shown how CDA methodology offers some refinements on some of the results and rigorous quantitative tools in order to confirm the original or offer novel hypothesis using compositional data. Note that biplots herein used improved the identification of variability patterns among the skull bones and constituted a more robust Principal Components Analysis than the similar one of the original work. Marugán and Buscalioni's paper has been reassessed as an example of how the quantification of variation arrays,

introducing CDA variables instead of the percentages, may deal with studies on Morphological Integration, performing regression analysis and testing hypothesis on Modularity. It may also be noticed that outliers detection through the CDA revealed distinct results that can be used as a re-sampling criterium or, depending on the specific objectives, as a preliminary indicator for further analysis on the atypical species.

Finally, Aitchison Distance (A.D.) is herein used as a valid metric of disparity in morphospaces using compositional data. After performing the adequate numerical transformations, compositional data can be analyzed in order to evaluate patterns of morphospace occupation as well as recognition of taxa trajectories in ternary diagrams.

3.1.1 Materials

A metric comparison of diverse fossil and extant Archosauria taxa was performed on the proportions of three constituent skull units: braincase, orbit and rostrum (figure 3.1). The main objective of Marugán and Buscalioni (2003) was to evaluate the existence of an archosaurian skull geometry and to achieve an empirical morphospace within which to examine patterns of archosaur skull design. The data used in the original analysis are compositional; these are proportions and should follow the procedures of CDA - recall chapter 2.

A sample of 153 specimens, compiled from the Marugán and Buscalioni database, was analyzed, but it was decided not to include two specimens from the original sample in this analysis - *Euparkeria capensis* and *Scleromochlus taylori* – because they are single specimens of its corresponding taxa and invalidate most of the statistical analysis performed.

3.1.2 Biplots

The *rostrum* proportion has a strong influence on the first principal component (PC1=80%) and represents the largest relative variability (figure 3.2). The orbit and braincase proportions present lesser and almost identical relative variability (slightly bigger for the braincase) and have identical influence on both the first and second components.

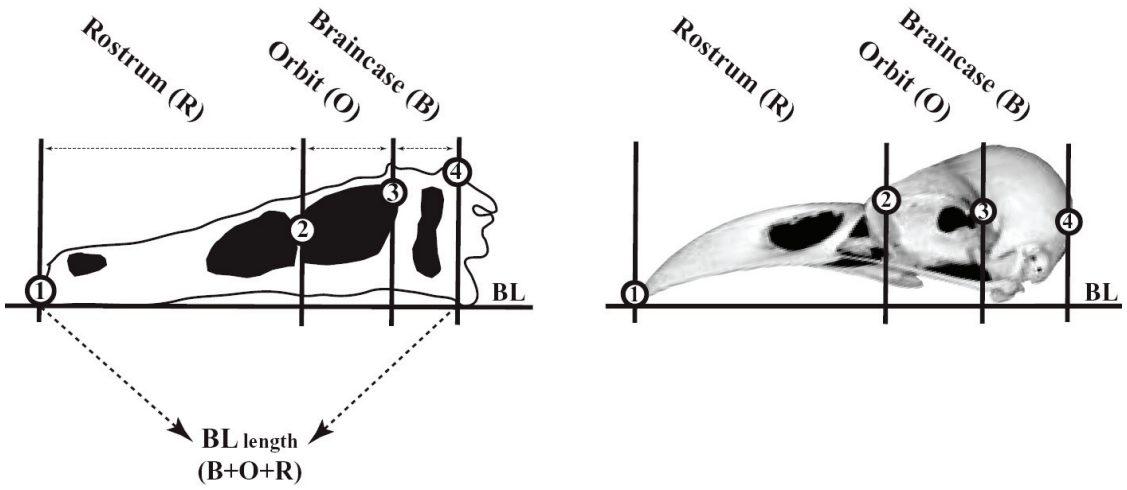

Figure 3.1 Skull parts used in the Marugán and Buscalioni paper. Lateral views of the theropod dinosaur *Velociraptor mongoliensis* and the modern bird *Corvus corax*. 1–4 are landmarks and measures taken for R (rostrum), O (orbit) and B (braincase). BL denotes baseline length (B+O+R). Description of landmarks is given in Marugán and Buscalioni (2003, fig. 3A).

The non-discriminated sample biplot has a large dispersion of specimens in every group. This fact prevents a precise discrimination of groups by the principal components identified. Despite this, Pterosauria and Ornithischia could be roughly distinguished on basis of PC1, which is directly associated with the variability of rostrum proportion.

The variation array and the percentages of variance for each element and biological group as well as the biplot indicate that more than half of the total variance originates from the rostrum proportion (53.2%), followed by the proportions of the

braincase and orbit – 26.4% and 20.4%, respectively (tables 3.3 and 3.4, figure 3.2). The variation array of the non-individualized sample indicates that the larger values of logratio variance appear when rostrum part is involved – 0.373 with braincase and 0.325 with orbit.

Further analysis and discussion of variability for each bone skull on the individual taxa will be performed further in this chapter.

	B	O	R	*clr* var	% Var
B		.109	.373	.071	**26.4**
O	-.043		.325	.055	**20.4**
R	-1.265	-1.222		.143	**53.2**
Total variance = 0.269					

Table 3.1 Variation array for the Marugán and Buscalioni (2003) complete data set. Abbreviations: B - braincase; O – orbit; R – rostrum.

Individualized Taxonomic Variance

The biplots, as well as the variation arrays for the individualized taxa, have been computed in order to evaluate if the variance patterns among the three skull parts were consistent with the whole sample analysis. It was decided only to inscribe the variance percentages of each taxa's individual bone. The decision of combining 'Prosauropoda' and Sauropoda was based on both sample size and taxonomical proximity comparatively to the other taxa.

The biplots for the individualized taxa, similar to the whole sample biplot, suggests that the rostrum proportion is, in all groups, the skull element that most strongly influences total variability - figure 3.3. a, b, c, d and e.

In Theropoda the rostrum influence is not as significant as in other groups, because the orbit presents similar influence in the total variability. This fact could be observed as well in the biplot, in which the lengths of all rays are almost identical (figure 3.13. c). Completing this and by looking at table 3.3, one detects that the variances of rostrum and orbit are almost identical – 36% and 34.9%, entailing that the

three bone proportions have equivalent influence in the total quantified variability. Confirming this, one observes that in the theropods the first two principal components display percentages of explained variance which are very similar – 53 and 47, respectively. Theropods reveal that PC1 is influenced both by the rostrum and the orbit proportions. One also detects that the braincase proportion has a strong influence and is clearly linked with PC2 in theropods.

This evident influence on PC2 is also identifiable in Sauropodomorpha, even if in this group that relationship is related to the orbit proportion. Sauropodomorpha is the group where one could identify the strongest influence of the braincase in the total variability – 40.3%, as it can be confirmed in the variances table for the individualized taxa - table 3.2.

Comparing the biplots of closely related taxa such as theropods and birds, one notices that in the latter most of the variability among individuals is due mainly to rostrum proportion, while in the non-avian dinosaurs the process of variability is not so linear. The more evident difference comes from a larger influence of the orbit on the total variability in theropods and also from a reduction of the rostrum determination in the total variability of theropods, which present a more conservative variability pattern regarding this bone than birds.

In most of the groups, PC1 is affected primarily by the rostrum proportion, namely on the Aves biplot – figure 3.13. d, in which that influence is very clear. The rostrum proportion weight on PC1 diminishes gradually throughout Ornithischia, Pterosauria, and Sauropodomorpha, reaching a minimum in Theropoda.

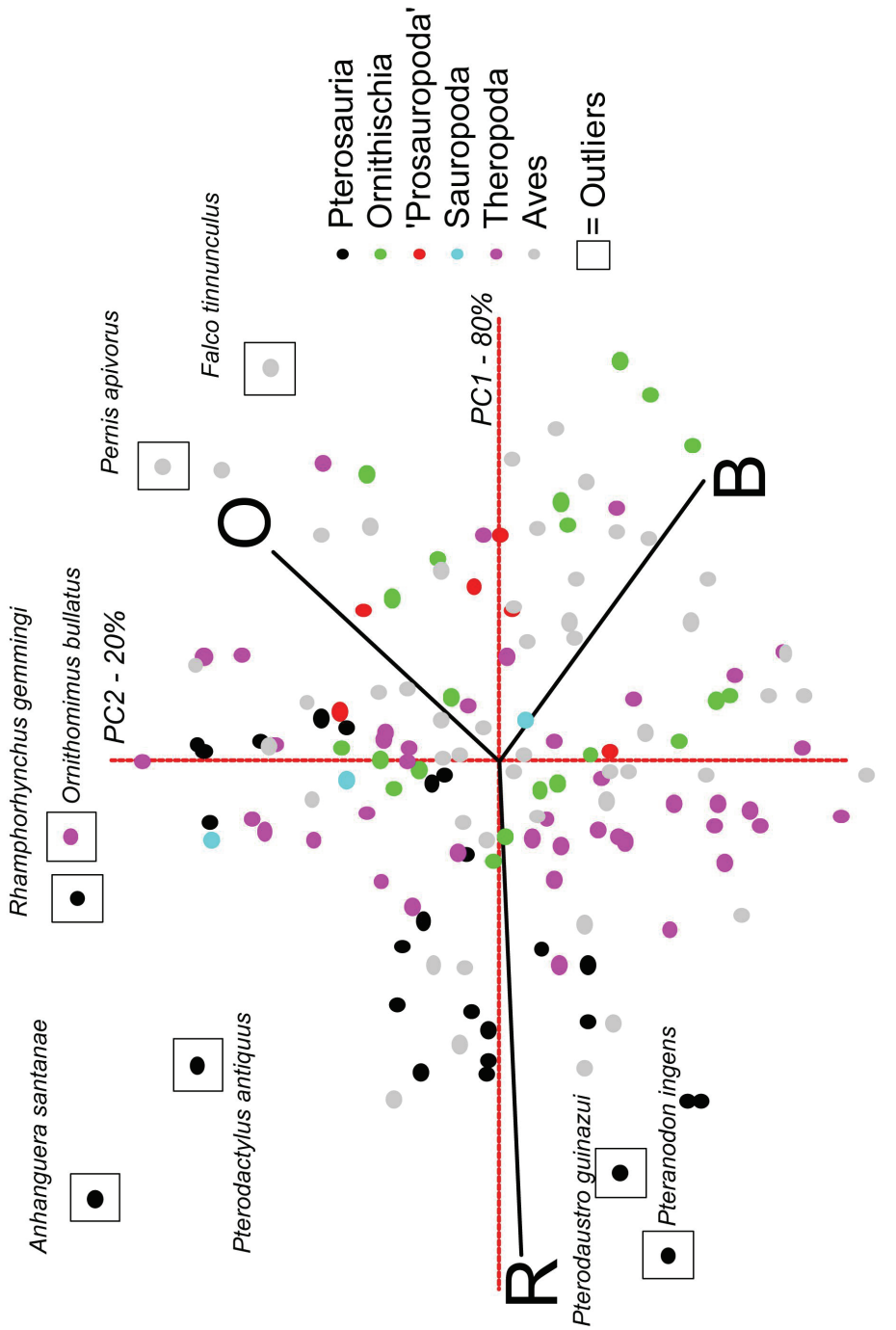

Figure 3.2 Biplot of the *clr*-transformed space of the first two principal components (PC1 vs PC2) of Pterosauria, Ornithischia, 'Prosauropoda', Sauropoda, Theropoda and Aves, skull elements. First principal component (80%), Second principal component (20%). Outliers – indicated in figure as squares. Abbreviations: R – rostrum; B – braincase; O – orbit.

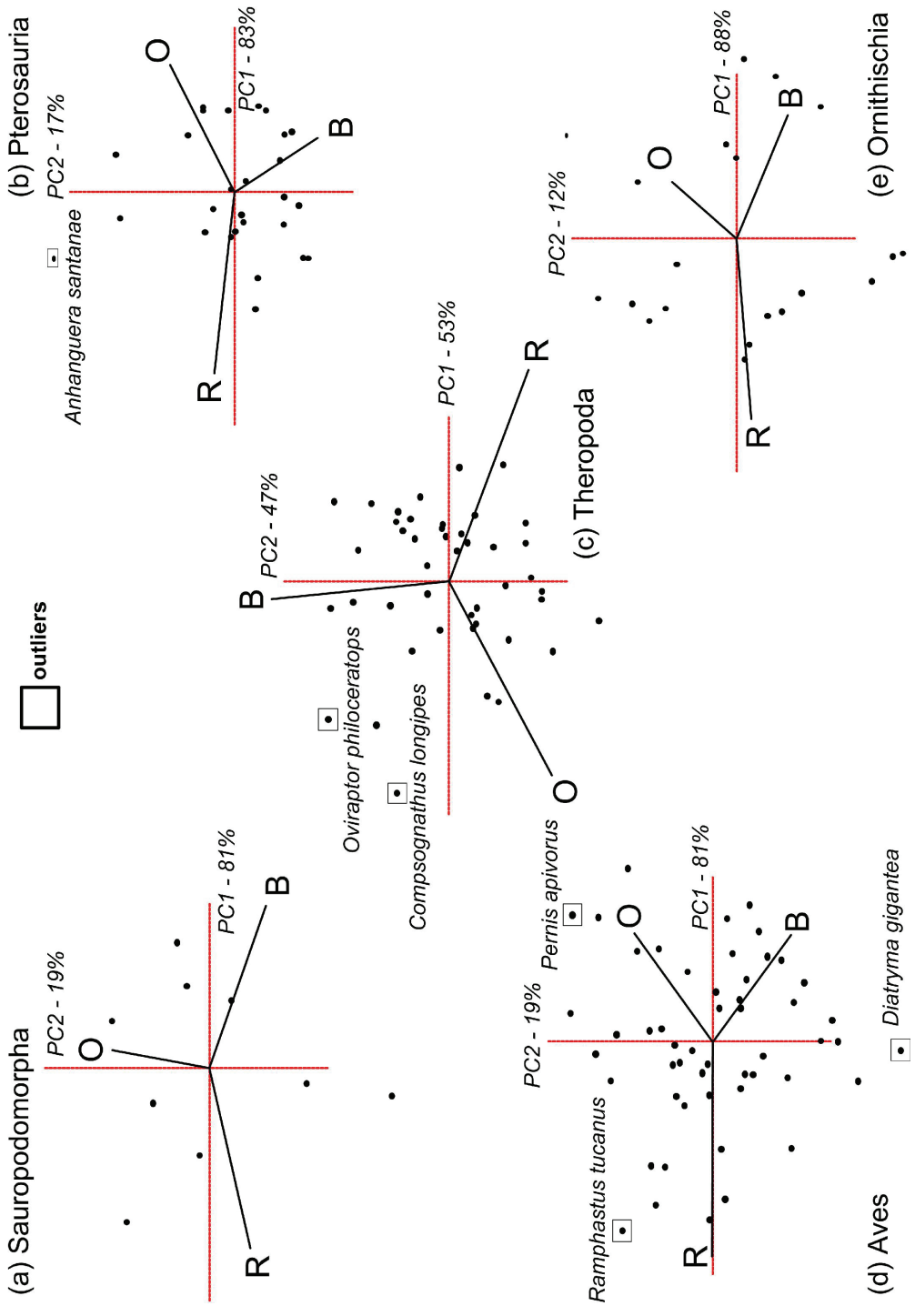

Figure 3.3 Biplots of the *clr*-transformed space of the first two principal components (PC1 *vs* PC2) of individualized taxa, a) Sauropodomorpha ('Prosauropoda'+Sauropoda), b) Pterosauria, c) Theropoda, d) Aves and e) Ornithischia skull elements. First Principal Component and second Principal Component percentages of explained variance are indicated. Outliers – indicated in figure as squares. Abbreviations: R – rostrum; O – orbit; B – braincase.

Apart from the aforementioned particular situations of sauropodomorphs and theropods, PC2 is affected mostly by a combined and minor influence of orbit and braincase proportions. This combined influence is also noticed in most of the groups regarding PC1. This pair of skull bones seems, therefore, to have a compound effect on the total variability in most of the groups.

The results presented in table 3.2 allow us to identify that the variance pattern and relationship between the three skull parts is not maintained when one analyzes the individualized taxa.

TAXA n=153	**Pteros.** n=27	**Aves** n=52	**Thero.** n=44	**Ornit.** n=21	**Sauro.** n=9	**Total sample**
B (% var)	14.9	22.6	29.1	30.7	40.3	26.4
O (% var)	31.8	23.1	34.9	12.6	13.0	20.4
R (% var)	53.3	54.3	36.0	56.7	46.7	53.2
Total variance	.229	.256	.148	.201	.100	.269

Table 3.2 *Clr* variance of the the bone parts for each group for Marugán and Buscalioni 2003 complete and individualized taxa data set. Abbreviations: B - braincase; O – orbit; R – rostrum; Ornit. – Ornithischia; Ptero. – Pterosauria; Sauro. – Sauropodomorpha (Prosauropoda+Sauropoda); Thero. – Theropoda; var - variance.

Aves reveal the biggest variance among all groups, followed by Pterosauria and Ornithischia. Although the sample sizes of sauropodomorphs and theropods are different, their total variances are somewhat equivalent, being the latter group more variant than the former. Comparing the percentages of variance for each skull bone and every taxa and applying a similar method one also notices differences within the non-discriminated sample. The most variant bone in every group is the rostrum, ranging from 56.7% of the total variance in Ornithischia to the lower values of 36% in Theropoda and 46.7% in Sauropodomorpha. In the remaining groups, Pterosauria and Aves, more than half of the total variance is due to the rostrum proportion.

The second most influential bone proportion in the total variance is the orbit, in most of the taxa except in Ornithischia and Sauropodomorpha, in which the braincase variance surpasses the orbit. The orbit variances in the Pterosauria and Theropoda are

analogous, with more than 30% of the total variance, being the carnivorous dinosaurs the group which reveals a bigger value of orbit variance – 34.9% of the total. Aves display 23.1% of orbit variance, a value almost identical to the one this group shows for the braincase variance, i.e., 22.6% of the total.

Concerning the braincase proportion on the total variance, this skull unit is more dissimilar in sauropodomorphs, 40.9%, and in Ornithischia, 30.7%, and constitutes less than a third of the total variance in the remaining groups, with a smallest value of 14.9% in Pterosauria.

3.1.3 Centering

As previously described, ternary diagrams are used in different fields of biological sciences in order to explore sets of compositional data. They allow visualizing compositional data characterized by three or more components. Difficulties and erroneous interpretations of this compositional data come up when compositions are close to the boundaries of the ternary diagram. These pitfalls are illustrated by a particular figure from Marugán and Buscalioni (2003: fig.4-A, p.73). The authors started their analysis of the skull geometry with a representation of the compositional data – skull element lengths – in a ternary diagram, used in this study as an empirical morphospace which was applied as an exploratory tool for studying the relative contribution of the three elements simultaneously.

The figure from the original data was recomputed in two versions: non-centered and centered ternary diagrams (figure 3.4 a and b). Marugán and Buscalioni identified, in a non-centered ternary diagram, a linear trend among all group clusters. This trend was identified as going from the center of the diagram towards the braincase minimum apex. In the non-centered representation - 3.4 a - the pattern of the data might look like a linear trend in the usual Euclidean sense. Marugán and Buscalioni (p.72) refer “Two main axes can be defined over the region” and “an operative expression for the rostral variation over the morphospace”.

After performing a centering operation (Martín-Fernández et al. 1999) one could detect a larger dispersion of the data with no clear linear trend for most of the groups (figure 3.4 b). It could also be observed that the referred main axis of variation and the categorical rostral range of proportion, although existing, is less identifiable as previously referred.

It is therefore essential, in order to identify and interpret the patterns, to center the compositional data. These methodological concerns are of special importance when all data or a subsample of it are placed near the boundaries of the ternary diagram.

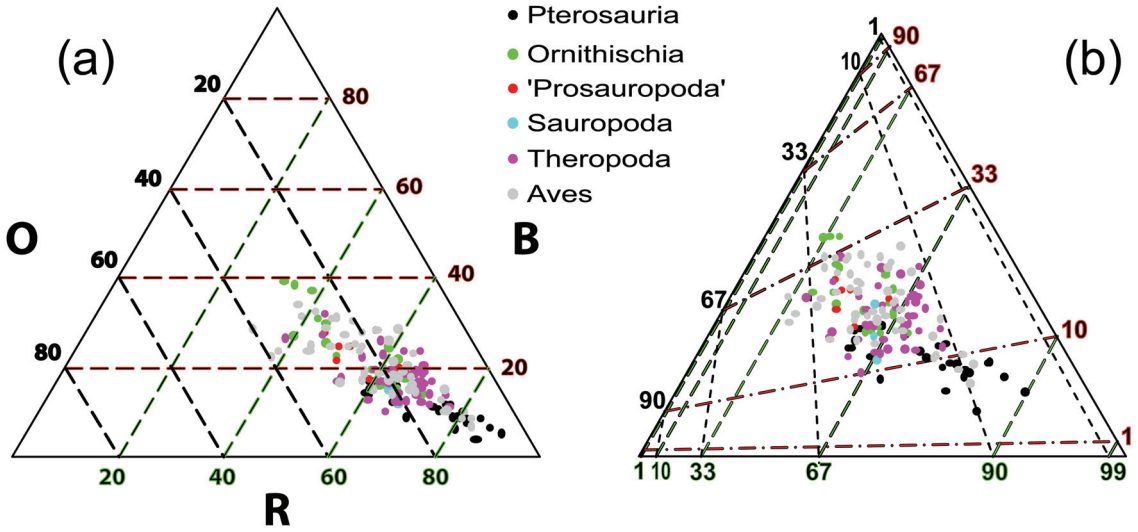

Figure 3.4 Marugán and Buscalioni (2003) (a) non-centered and (b) centered data ternary diagrams. Center of the original data set B – 18%; O – 19%; R – 63%.

3.1.4 Correlation analysis

Marugán and Buscalioni plotted bivariate scatterplots in order to test correlations between the braincase, orbit and rostrum proportions. The performed analysis identified strong negative correlations, and all significant, between braincase and rostrum proportions, within all samples and on the individual taxa. The same analysis was performed for the orbit and rostrum proportions with similar results.

Although an equivalent correlation analysis with the CDA transformed data could be performed, the clr-correlation analysis makes little sense, since the covariance matrix is singular and the clr-axis are not orthogonal.

Outliers

Several atypical observations (outliers) were identified employing the proportions parts and using it as atypicality indices under the assumption of the Additive Logistic Normal (ALN) distribution. The ALN distribution was tested using the battery of tests proposed by Aitchison (1986). The threshold of atypicality used to identify the outliers was 0.95 and permited the identification of the following outliers for the braincase and orbit proportions of the complete sample: *Albertosaurus libratus*, *Anhanguera santanae*, *Diatryma gigantea*, *Ornithomimus bullatus*, *Ornithomimus samueli*, *Phalacrocorax aristotelis*, *Pterodactylus antiquus* and *Rhamphorhynchus gemmingi*.

The atypical specimens mostly belong to Theropoda, Pterosauria (three pterodactyloids and two rhamphorhynchoids) and Aves. If one recalls fig. 4-C of Marugán and Buscalioni (2003, p.73), one detects different results between that non-CDA methodology and the CDA used herein, although also detecting identical outliers, namely *A. libratus*, *O. bullatus*, *R. gemmingi* and *A. santanae*.

It could be stated that the braincase-orbit proportions atypical identification of the individualized sub-sample reveals only four common specimens using the two methodologies: *A. santanae*, *O. bullatus*, *P. aristotelis* and *R. gemmingi*[*].

The non-CDA approach only reveals two outliers, theropods *C. longipes* and *O. philoceratops*. Far more atypical species are identified when one uses the *clr* data transformation. For the complete sample the outliers are: *Albertosaurus libratus*, *Anhanguera santanae*, *Diatryma gigantea*, *Falco tinnunculus*, *Ornithomimus bullatus*, *Pernis apivorus*, *Pteranodon ingens*, *Pterodactylus antiquus*, *Pterodaustro guinazui* and *Rhamphorhynchus gemmingi* (table 3.4).

[*] Please bear in mind that the outlier identification for the individualized taxa indicates that those specimens are outliers only within its group and not in the non-discriminated sample, like in Marugán and Buscalioni's paper or on this work's non-discriminated sample comparison.

The equivalent comparison now performed within each group reveals less atypical specimens but nevertheless more than the non-CDA analysis: *Anhanguera santanae*, *Compsognathus longipes*, *Diatryma gigantea*, *Oviraptor philoceratops*, *Pernis apivorus* and *Ramphastus tucanus*, the latter not being recognized as an outlier in the computation of the non-discriminated sample.

The outliers for the three skull parts have been computed, both for the non-discriminated sample and for the individualized one. The identification of outliers was also computed for the different pairs of bones both for the non-discriminated sample and for the individualized one.

These computations, compiled in table 3.3, allow some considerations:

- Sauropodomorpha does not present any outlier in the complete sample analysis and within its group only *Diplodocus longus* is considered as atypical for the comparisons of braincase-orbit and braincase-rostrum proportions. This indicates that this species braincase proportion could be the disturbing factor, since it is the common element in the referred comparisons;

- *C. longipes* is one of the outliers within its group and when comparing the three bone proportions. Computing the various dual comparisons of skull bones one detects that *C. longipes* is classified as outlier within Theropoda for the braincase-rostrum and orbit-rostrum proportions and is not considered as atypical for the braincase-orbit proportions. Thus, it could be inferred that *C. longipes* presents a rostrum proportion so dissimilar among theropods that it implicates its atypicality;

- the bird *D. gigantea* is classified as an outlier in all of the CDA analysis, except in the individualized group analysis for both braincase-rostrum and orbit-rostrum proportions;

- five pterosaurs are considered as outliers for the combined analysis of the three proportions of non-discriminated sample - *Pteranodon ingens*, *P. antiquus, Pterodaustro guinazui*, *R. gemmingi* and *A. santanae* - but only the latter remains an outlier when

comparing the three parts within the pterosaur sample. *A. santanae* is classified as an outlier in every analysis and combination of bones, except in the orbit and rostrum proportions within pterosaurs. Therefore, *A. santanae* is an outlier due mainly to the braincase proportion;

- the only ornithischian regarded as an outlier is *Psittacosaurus meileyungensis* in the individualized taxa comparison of the braincase-rostrum proportions;

- the theropod *O. bullatus* is always an outlier when one compares the complete sample, but within its group it is only considered atypical when we are comparing the braincase-orbit proportions;

- the only theropod previously identified as an outlier, namely in Marugán and Buscalioni comparison of braincase-rostrum proportions and corroborated by the CDA of the complete sample computation was *A. sastrei*. This species, however, is not classified as an outlier in any of the comparisons made of pairs of bones proportions within its group;

- *Oviraptor philoceratops* is always regarded as atypical within Theropoda, except when comparing the orbit-rostrum proportions;

- *Ramphastus tucanus* is regarded as an atypical species within its group only in the braincase-rostrum proportion comparison.

Also:

- outliers classified by the CDA methodology of the non-discriminated sample are identical whatever the pair of bones compared and also when one examines simultaneously the braincase, orbit and rostrum proportions – see biplot in figure 3.2 and table 3.3;

- analyzing the individualized taxa sample, differences among the distinct pairs of bones and the three parts comparisons could be recognized. One notices that Aves is the group with the higher number of outliers in most of the comparisons, except in the braincase-rostrum proportions. In this case, the number of birds outliers is equaled by

the theropods. One also detects that birds species considered as atypical vary depending on which pair of bones one includes in the analysis.

Outliers[1]	Marugán and Buscalioni (non-CDA)	This work (*clr* of complete sample)	This work (*clr* of individualized taxa)[3]
B-O	*Aegypus monachus* (A) *Albertosaurus libratus* (T) *Anhanguera santanae* (P) *Carnotaurus sastrei* (T) *Dromaeosaurus albertensis* (T) *Gyps fulvus* (A) *Ornithomimus bullatus* (T) *Phalacrocorax aristotelis* (A) *Porphyrio mantelli* (A) *Ramphorhynchus gemmingi* (P) *Tyrannosaurus rex* (T)	*Albertosaurus libratus* (T) *Anhanguera santanae* (P) *Diatryma gigantea* (A) *Ornithomimus bullatus* (T) *Ornithomimus samueli* (T) *Phalacrocorax aristotelis* (A) *Pterodactylus antiquus* (P) *Rhamphorhynchus gemmingi* (P)	*Anhanguera santanae* (P) *Diatryma gigantea* (A) *Diplodocus longus* (S) *Ornithomimus bullatus* (T) *Phalacrocorax aristotelis* (A) *Rhamphorhynchus gemmingi* (P)
B-R		*Albertosaurus libratus* (T) *Anhanguera santanae* (P) *Diatryma gigantea* (A) *Ornithomimus bullatus* (T) *Ornithomimus samueli* (T) *Phalacrocorax aristotelis* (A) *Pterodactylus antiquus* (P) *Rhamphorhynchus gemmingi* (P)	*Anhanguera santanae* (P) *Compsognathus longipes* (T) *Diplodocus longus* (S) *Eoraptor lunensis* (T) *Limosa limosa* (A) *Oviraptor philoceratops* (T) *Platalea leucorodia* (A) *Psittacosaurus meileyungensis* (Or) *Ramphastus tucanus* (A)
O-R		*Albertosaurus libratus* (T) *Anhanguera santanae* (P) *Diatryma gigantea* (A) *Ornithomimus bullatus* (T) *Ornithomimus samueli* (T) *Phalacrocorax aristotelis* (A) *Pterodactylus antiquus* (P) *Rhamphorhynchus gemmingi* (P)	*Compsognathus longipes* (T) *Falco tinnunculus* (A) *Pernis apivorus* (A) *Platalea leucorodia* (A) *Pteranodon ingens* (P)
B-O-R	*Compsognathus longipes* (T)[2] *Oviraptor philoceratops* (T)	*Albertosaurus libratus* (T) *Anhanguera santanae* (P) *Diatryma gigantea* (A) *Falco tinnunculus* (A) *Ornithomimus bullatus* *Pernis apivorus* (A) *Pteranodon ingens* (P) *Pterodactylus antiquus* (P) *Pterodaustro guinazui* (P) *Rhamphorhynchus gemmingi* (P)	*Anhanguera santanae* (P) *Compsognathus longipes* (T) *Diatryma gigantea* (A) *Oviraptor philoceratops* (T) *Pernis apivorus* (A) *Ramphastus tucanus* (A)

Table 3.3 Comparison of outliers identified by the Marugán and Buscalioni (2003) analysis and the two CDA herein computed. Abbreviations: B- braincase; O- orbit; R- rostrum; A- Aves; Or- Ornithischia; P- Pterosauria; S- Sauropodomorpha; T- Theropoda. [1] - The B-R and O-R outliers were not clearly identified in Marugán and Buscalioni (2003). [2] - The cited species are outliers when compared by groups in the original analysis. [3] - In this analysis the "Prosauropoda" and Sauropoda are combined as Sauropodomorpha.

3.1.5 Aitchison Distances (A.D.) - disparity metrics

The disparity index used by Marugán and Buscalioni (2003) lies on the quantification of the morphospace occupied. This evaluation was performed by counting the number of triangles occupied by the specimens (Marugán and Buscalioni 2003, p.71 and fig. 4A).

This option is not numerically coherent, since changing the number of subtriangles in the ternary morphospace implicates different areas of occupied morphospace and, therefore, different disparity results.

In this work the previously introduced A.D. will be used as a measure of disparity. The intergroup A.D.† for the braincase, orbit and rostrum proportions represents the distances between group centroids. It serves as an indicator of the relative interval between group centroids when working with compositional data such as skull bones proportions.

The group most distant from all the others is Pterosauria, a fact which could be interpreted as a result of its phylogenetic position outside Dinosauria - table 3.4. The most distant group from pterosaurs is Prosauropoda, with an A.D. of 0.858, followed by Ornithischia and Aves, with Aitchison distances of 0.810 and 0.673, respectively.

In contrast, the groups with the closest proportions are Prosauropoda and Ornithischia, with an A.D. of 0.100, followed by Aves and Ornithischia, with an A.D. of 0.139, and Aves and Theropoda with an A.D. of 0.176. These facts are intriguing, as birds and theropods are phylogenetically close but have larger A.D. than the more phylogenetically distant ornithischians and birds.

Sauropodomorph groups, i.e. ‘Prosauropoda’ and Sauropoda, which are also phylogenetically closely related, reveal distinct A.D.. The groups closest to sauropods in morphospace are theropods (A.D. =0.208) and birds (A.D. =0.287). The most distant are ‘prosauropods’ and pterosaurs, with A.D.s of 0.412 and 0.472, respectively - table 3.4.

Although numerically rigorous and constituting an important enhancement on the visual only aspects of non-CDA analysis of ternary diagrams, intergroups A.D. do not inform us on how the specimens are positioned within the compositional morphospace or how dispersed specimens are within a group.

† Recall section 2.2.3 for further explanation on the A.D.

The intergroups should be taken into account after performing an exploratory analysis and the computations of the intragroups A.D., which are both more informative on the patterns of morphospace occupation, as well as on the variation among the parts.

	Ptero.	Ornit.	Prosau.	Sauro.	Thero.
Ornithischia	.810				
Prosauropoda	.858	.100			
Sauropoda	.472	.396	.412		
Theropoda	.501	.315	.380	.208	
Aves	.673	.139	.212	.287	.176

Table 3.4 Intergroup A.D.s of the three skull proportions. The A.D. represents the distance between group centroids. Abbreviations: Ornit.–*Ornithischia*; Prosau.–*Prosauropoda*; Ptero.- *Pterosauria*; Sauro.- *Sauropoda*; Thero.- *Theropoda*.

The intragroups A.D., which correspond to the distance of each specimen regarding the centroid of its group, have been computed. For each group several statistical descriptive indices were calculated and indicated in table 3.5. Among those indices are the mean of the intragroups A.D. within a group, as well as the corresponding variance and the maximum value, which are all informative in the patterns of variability of the individuals among a group. The variance for each skull bone within a group has also been calculated.

Intragroups A.D.	**n**	**Mean**	**var**	**Max.**	**B** *clr* var	**O** *clr* var	**R** *clr* var
Pterosauria	**27**	.462	.036	.800	.034	.073	.122
Ornithischia	**21**	.288	.018	.547	.062	.025	.114
Prosauropoda	**6**	.369	.024	.642	.016	.017	.031
Sauropoda	**3**	.328	.003	.372	.046	.009	.014
Theropoda	**44**	.321	.030	.872	.043	.052	.053
Aves	**52**	.473	.066	1.058	.058	.059	.139

Table 3.5 Intragroups A.D. mean, variance (var) and maximum (Max.); variance (var) for each skull element: B - braincase; O – orbit; R – rostrum.

Considering the mean intragroup A.D.s as a measure of group disparity, it is clear that the most disparate group is Aves, followed by Pterosauria and Prosauropoda, with mean A.D.s of 0.473, 0.462 and 0.369, respectively. Ornithischia is the more conservative group considering the mean distance of its species to the centroid of the three elements proportions, with a mean A.D. of 0.288, followed by the successively bigger A.D. of Theropoda and Sauropoda.

Sauropodomorphs, i.e., Prosauropoda and Sauropoda, reveal reduced variances, which might be explained by the low taxonomical sampling in Marugán and Buscalioni's (2003) original dataset.

Although showing small mean A.D., theropods reveal considerable variability among individuals, as well as a high maximum value. These facts imply that this group presents a reduced dispersion of the specimens in the morphospace, even though having some dissimilar elements in its structure. The impossibility of an adequate sampling within all sub-clades of theropods could be the statistical bias.

In contrast, Aves and Pterosauria have large dispersion in the proportions' morphospace, a fact corroborated by the large variances and maximum values detected. Comparing the close related taxa of theropods and birds, one observes that the theropods present a more conservative pattern in the morphospace – A.D. 0.312 – than the birds – A.D. 0.473.

Also represented in table 3.5 is the *clr* variance for each skull part. The variance is higher on the rostrum portion of the skull in every group, except in sauropods, in which the skull element with higher disparity is the braincase – the variance is 0.046. Despite this, it should be noted that in theropods the variance of the rostrum and orbit proportions is almost identical – 0.053 and 0.052, respectively.

The less dissimilar (i.e., more conservative in terms of proportion) skull elements among individuals of a group are the braincase – in Pterosauria, Prosauropoda, Theropoda and Aves – or the orbit – in Ornithischia and Sauropoda.

One should bear in mind that regarding Prosauropoda and Aves, the braincase and orbit proportions variance is almost identical, meaning that the braincase and orbit present a pattern of proportions more conservative than the rostrum.

Recalling the variation array of the non-discriminated total sample, one could corroborate that the most variant region of the skull is the rostrum – with 53.2% of the total variation, followed by the braincase and the orbit – see table 3.1.

Focusing on groups variability, one notices that the most disparate is Aves, followed by Pterosauria and Ornithischia, with mean intragroup A.D.s of 0.473, 0.462 and 0.369, respectively.

A.D. Outliers

Recall that *Psittacosaurus meileyungensis* has been considered as an outlier for the braincase-rostrum proportions in Ornithischia in the identification of atypical specimens represented in figure 3.2 and in table 3.3.

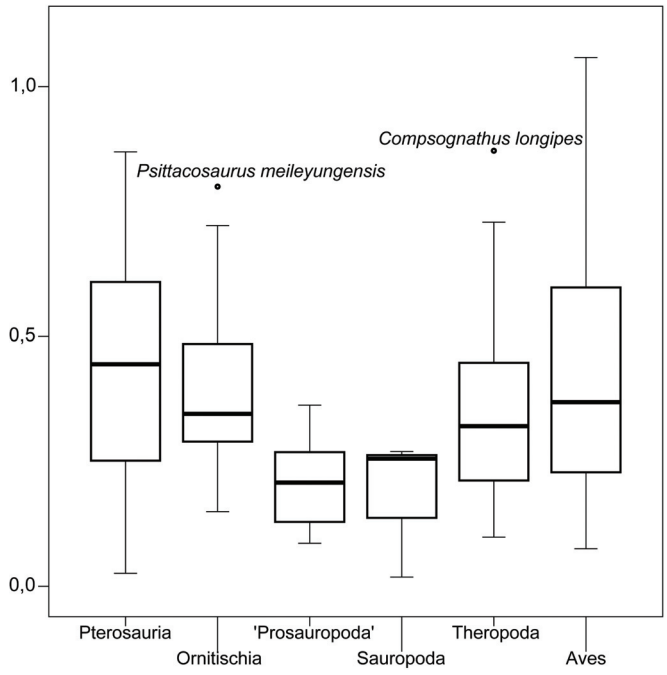

Figure 3.5 - Box plot of intragroups A.D. Outliers for the individualized taxa are indicated.

Using now the A.D. as an atypicality index, this species is again classified as an outlier. The two types of information allow us to state that this species is atypical

within its group due fundamentally the braincase proportion which is the biggest among the three analyzed skull bones

Intragroups A.D. also allows identifying *Compsognathus longipes* as an outlier within theropods, which had not been noted previously.

3.1.6 FINAL REMARKS

The present review and reanalysis of the dataset presented by Marugán and Buscalioni (2003) allows refinement and further exploration of the patterns of skull shape within archosaurs.

Applying the robust CDA methodology permits:

- the recognition that the linear trends referred in the skull morphospace are not as evident as originally stated;

- a correction in the identification of outliers in skull bone proportions;

- the introduction of a measure of morphological disparity, Aitchison Distance, which in turn allows a precise index of comparison of taxa and specimens in proportions' morphospaces;

- the identification of contrast variability patterns among the skull parts.

3.2. "Limb disparity and wing shape in pterosaurs"

G.J. Dyke, R. L. Nudds and J.M.V. Rayner (2006)

and

"A morphospace-based test for competitive exclusion among flying vertebrates: did birds, bats and pterosaurs get in each other's space?"

A.J. Mcgowan and G.J. Dyke (2007)

The limb elements proportions from the above cited works have been used to infer biomechanic similarities and differences across three flying vertebrate groups - birds, pterosaurs and bats.

While the main objective of McGowan and Dyke 2007 was to assess the existence of competitive exclusion among extinct and living flying vertebrates, using fore and hind limb measurements in order to construct morphospaces, the paper from Dyke et al. 2006 aimed, in general terms, to discriminate the "bird-like" mode (only fore limb involved) or "bat-like" mode (both fore and hind limb) of pterosaur flight - see below pterosaur functional description in order to compare the two paradigms of pterosaur flight. In that paper, Dyke and colleagues employ *Sordes pilosus* - one of the few pterosaur specimens with flight membrane preserved - as a model, in order to contrast both pterosaur flight paradigms: bat-flight or bird-flight. In order to achieve it, the authors performed fore to hind limb ratios analysis and compared the pterosaur results with the two extant taxa. Also, Dyke et al. evaluated the occupation patterns of a proportions morphospace and established non-quantified similarities for the three flying vertebrates.

Flying vertebrates - general anatomical and functional characteristics

"Flight is hard to accomplish, but the rewards are great and clearly repay the effort."

Gee (2000, p.173)

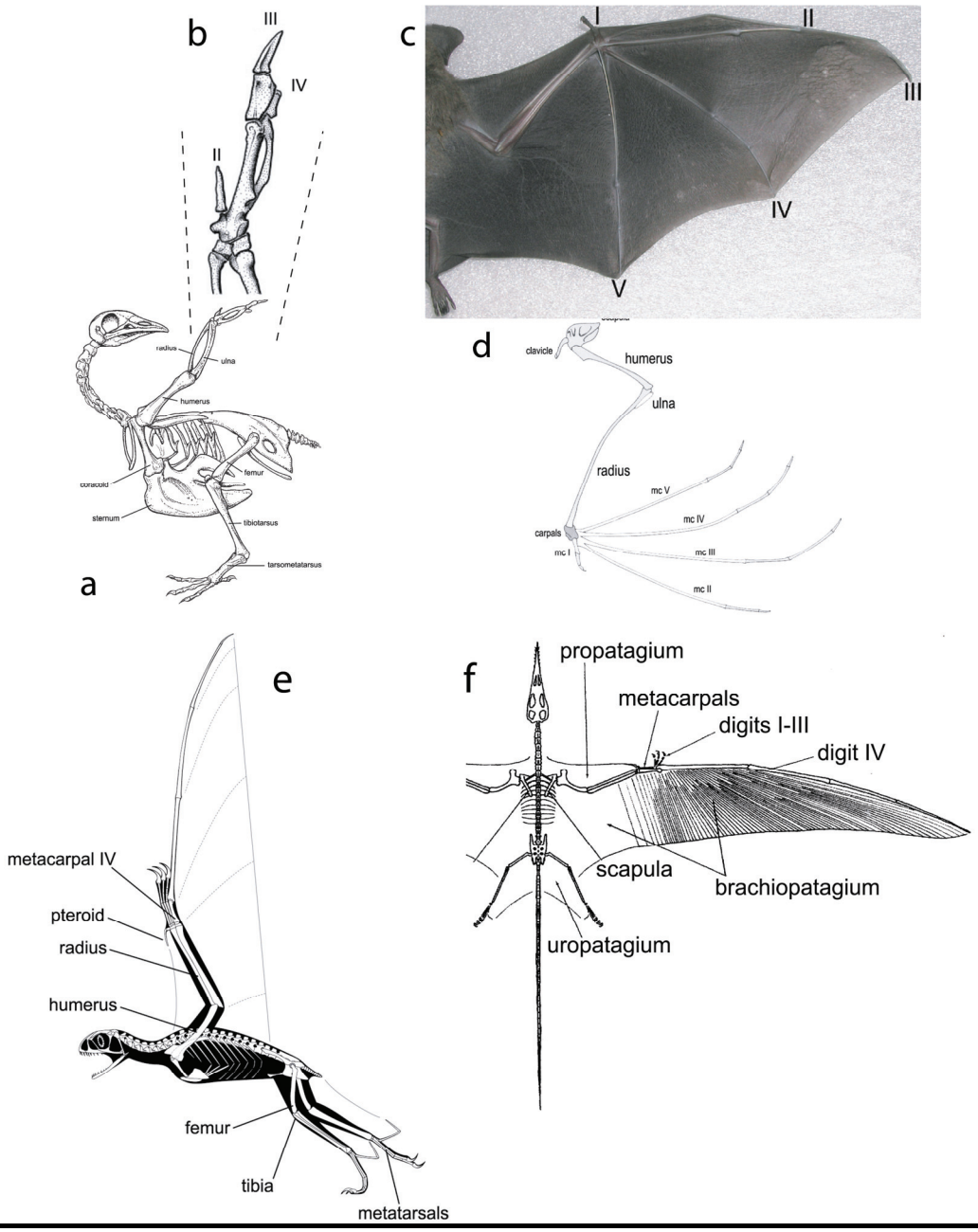

Figure 3.6 a) general morphology of an adult bird - adapted from Pettingill (1956); b) adult *Gallus gallus* wing with three ossified digits - adapted from Larsson and Wagner (2002); c) forelimb morphology an adult bat, *Carollia perspicillata* - adapted from Weatherbee (2006); d) forelimb osteology of an adult bat - adapted from Kent and Miller (1997); e) pterosaur *Jeholopterus ningchengensis* general appendicular morphology - adapted from Wang et al. (2002); f) pterosaur *Rhamphorhynchus muensteri* limbs and wing membrane morphology - adapted from Wellnhofer (1991).

Aves, contrary to the other flying taxa herein analyzed, have a flying module - the fore limb - independent from the hind limb and tail. Unlike bats and pterosaurs, the wings are not membranous, but composed of feathers. The birds' fore limb morphology reveals three ossified digits, in adults, being the longest the digit III. The debate concerning the homology of bird digits and pentadactyl amniotes is 200 years old and has two sources of arguments (Larsson and Gunter 2002): one comes from the fossil record and phylogenetic systematics that attributes homology to digits I, II and III; the other source originates in the embryology supporting digital homology of digits II, III and IV. The paleontological data shows a trend of reduction of the digits IV and V from the basal most theropods, where these digits are reduced but still exist, to Tetanurae, already bearing a tridactyl hand (Padian and Chiappe 1998).

Various non-autopodial elements of the fore limb suffered a reduction in size along birds' evolutionary history. Some authors establish an inverse correlation between humerus length and aerial maneuverability, that is, birds with longer humerus, like alcids, loons, cuckoos, grebes, and albatrosses are poor maneuvering fliers (Middleton and Gatesy 2000; 2006).

Bats comprise about one-quarter of the present mammalian diversity, and possess non-pneumatized, narrow-filled long bones (Nowak 1991), the humerus and radius revealing a thin-walled morphology (Swartz et al. 1992). The fore limb zeugopodium of bats is dominated by radius, since the ulna is vestigial. Chiroptera wings comprise a membrane supported mainly by the II-V fore limb digits, but also by the hind limb. Bat wings, therefore, are involved by a fold of skin – patagium - supported by elongated digit bones and, in the suborder Microchiroptera, a clawed digit I is present. The single-family suborder Megachiroptera reveals claws on the digits I and II. Concerning the flying membrane, the present work follows Simmons and Conway (2001), stating that "The wing membrane of bats is divided into the plagiopatagium (which extends between the body and the fifth digit), dactylopatagium (which extends

between the digits), propatagium (which extends between the upper arm and forearm anterior to the elbow), and uropatagium (which extends between the hindlimbs)."

The extinct clade Pterosauria main morphological feature in the fore limb is the extreme development of digit IV, the correspondent metacarpal being generally longer in Pterodactyloidea and shorter in Rhamphorhynchoidea (Middleton and Gatesy 2006). This extremely developed digit supported the wing membrane that permitted pterosaurs active flight.

Another Pterosauria fore limb unique osteological feature is the existence of the pteroid, a bone associated with the support of the wing membrane - propatagium - and articulating with the carpal (Bennett 2006). Pterosaurs exhibit an extremely light bone construction and even those with huge wingspans of 12 meters, such as *Quetzalcoatlus* from North America (Lawson 1975), had bones with walls only 2 millimeters thick (Wellnhofer 1991).

The patagium can be divided into three areas: the propatagium, in front of the humerus and ulna, the brachiopatagium, between the fore and hind limbs; and the uropatagium, between the hind limb and the tail (Wellnhofer 1991) - figure 3.6, e and f. Some authors identified a probable membrane attachment in the hind limb that may have occurred in the fifth digit (Unwin and Bakhurina 1994).

The monophyletic Pterosauria clade is divided into two groups: Pterodactyloidea and the paraphyletic Rhamphorhynchoidea. Pterodactyloidea, from middle Jurassic to Late Cretaceous, were large animals with a wingspan ranging from 2 to 11 meters, which flew very differently from more primitive pterosaurs. Originally small, pterodactyloids developed morphological innovations in the fore limb as well as a reduction/lost of the tail that permitted a better functional performance than rhamphorhynchoids.

The Rhamphorhynchoidea pterosaurs, from Late Triassic to Early Cretaceous, could be characterized by its long tails, which conferred dynamic stability and a

considerable degree of maneuverability (Wellnhofer 1991; Witmer et al. 2003). Rhamphorhynchoids digit V is longer than digit I and some authors have argued that pedal digit V controlled the uropatagium and, therefore, was functionally implicated in pterosaur flight (Unwin 1988; Bakhurina and Unwin 1992).

Therefore, and concerning pterosaur flight, there are mostly two functional paradigms: one stating that wing membrane incorporates the hind limb (Unwin and Bakhurina 1994; Unwin 1999; 2006; Wellnhofer 1991) and the opposite paradigm, inferring that hind limb does not contribute to flight, due to the absence of wing membrane attachment in the hind limb (e.g., Padian 1983).

General purpose

To contrast the hypothesis formulated by McGowan and Dyke 2007 to discriminate flying amniotes, the following protocol using CDA analysis has been introduced:

1) estimating the centroid for the distinct analyzed taxa (fore and hind limbs);

2) computing diverse compositional numerical indicators, in order to explore the relative variation between the six parts (fore and hind limb elements);

3) building a ternary diagram to explore the morphospace distribution of flying amniotes, and assess both intragroup and intergroup Aitchison Distances (i.e., disparity metrics), in order to discriminate morphospace occupation patterns;

4) statistically testing the A.D. differences among groups;

5) statistically testing the different groups bone parts proportions, both in fore and hind limbs, as well as in the combined limbs.

Finally, a balances analysis was computed (Egozcue and Pawlowsky-Glahn 2005), in order to complement the previous methodological steps. This methodology allows quantifying and evaluating the relative variation of parts ratio, through the decomposition of variability of the involved bone parts, which is potentially interesting in contrasting some hypothesis. For example, one informative ratio of bone parts is the

brachial index (Howell 1944) - humerus to radius length ratio - used to infer power requirements in birds (Rayner and Dyke 2003), that is to say, bird wings with low BI have low moments of inertia, which should reduce power requirements. One of the selected balances is therefore the humerus to radius ratio - B3.

The analytical depth of the limbs CDA analysis for each group has been increased, introducing taxonomic subsets not performed in the referred original works, within Chiroptera (i.e., Megachiroptera and Microchiroptera), and exploring the variation array and biplots for pterosaurs (Rhamphorhynchoidea and Pterodactyloidea*)* and both Chiroptera groups.

3.2.1 Materials

The data analyzed in this work was selected from sets of measurements previously published (Dyke et al. 2006; Mcgowan and Dyke 2007). The sample comprises 955 specimens, as follows: 603 Aves non-Passerines, 97 Aves Passerines, 217 Chiroptera, 13 Rhamphorhynchoidea, 11 Pterodactyloidea and 14 Theropoda – see Dyke et al. 2006 supplementary material.

Since birds and non-avian dinosaurs are subsets from within the same larger clade, it was decided to include specimens (n=14) from Theropoda, in order to contrast patterns of morphospace occupation and to include a phylogenetical control. Theropoda specimens were selected due to the completeness of the limb elements required for this analysis and were collected from several databases - see Appendix II.

The Chiroptera sample was analyzed in Dyke et al. 2006 and Mcgowan and Dyke 2007 as a single group. In the present work this sample was divided, in some analyses, into two sub-samples, each corresponding to Chiroptera sub-orders: Megachiroptera and Microchiroptera. This option was taken after the realization, from preliminary results, that the Chiroptera sample should be analyzed in more detail. The following works were adopted: Burkitt (1995), Schutt and Simmons (1998) and Giannini and Simmons (2005), for the diverse bat specimens taxonomical setting.

The limb elements analyzed for each specimen are:

- fore limb: humerus, radius or ulna and metacarpal IV for pterosaurs, metacarpal III for theropds and bats and carpumetacarpus for birds;

- hind limb: femur, tibia and metatarsal III, for all groups.

The tarsal contribution to the tibia was included for all taxa, with the exception of Theropoda. In pterosaurs and bats, which present non fused feet, the length of metatarsal III has been used and considered the equivalent to the avian tarsometatarsus (Gatesy and Middleton 1997).

3.2.2 Centroid and Percentages on fore and hind limbs.

The geometric centroids for the distinct taxa analyzed both for the fore and hind limbs were calculated - table 3.6 and figure 3.7.

Geometric centers (%)	**Non-Passe.** (Fore / Hind)	**Passe.** (Fore / Hind)	**Theropoda** (Fore / Hind)	**Chiroptera** (Fore / Hind)	**Rhamphor.** (Fore / Hind)	**Pterodacty.** (Fore / Hind)
Stylopodium (H-F)	39 / 26	35 / 26	51 / 38	18 / 44	10 / 34	14 / 34
Zeugopodium (R/U-T)	39 / 46	42 / 44	32 / 40	30 / 47	15 / 46	18 / 50
Autopodium (MC-MT)	22 / 28	23 / 30	17 / 22	52 / 9	75 / 20	68 / 16

Table 3.6 Groups geometric centers, in percentage, for fore and hind limb elements. Abbreviations: Rhamphor. – Rhamphorhynchoidea; Pterodacty. – Pterodactyloidea; H - humerus; R/U – radius/ulna; MC - metacarpal III; F - femur; T - tibia; MT - metatarsal III.

For each limb element – stylopodium, zeugopodium or autopodium – there are groups that could be considered as extreme forms, that is to say, groups in which one of those elements represents more than 50% of the total limb length – recall section 2.1.2.

Theropods is the only group than could be classified as a fore limb *stylopodium* extreme form, that is, the humerus constitutes more than 50% of the total fore limb length. The intermediate bone constituents, radius/ulna or tibia, dominate only in the hind limb of Pterodactyloidea. This group of pterosaurs also reveals an extreme fore limb, in which the autopodial bone represents almost three quarters of the total anterior limb length. Therefore, pterodactyloids are the sole specimens which are considered extreme forms both in the fore and in the hind limbs.

Regarding the autopodium, bats and both pterosaur groups – rhamphorhynchoids and pterodactyloids – constitute extreme forms in the most distal bone element of the fore limb.

None of the groups reveals more than half of the total limb length in the hind limb autopodial element, being Passerines the closer one to that condition, with 30%.

The compositional variation array (Aitchison 1986) was calculated in order to explore the relative variation between the six parts. It could be observed that the larger values of the logratio variance appear when the parts MC or MT are implicated and the *clr* variances of those parts is 1.13, roughly 80% of the total logratio variance - table 3.7.

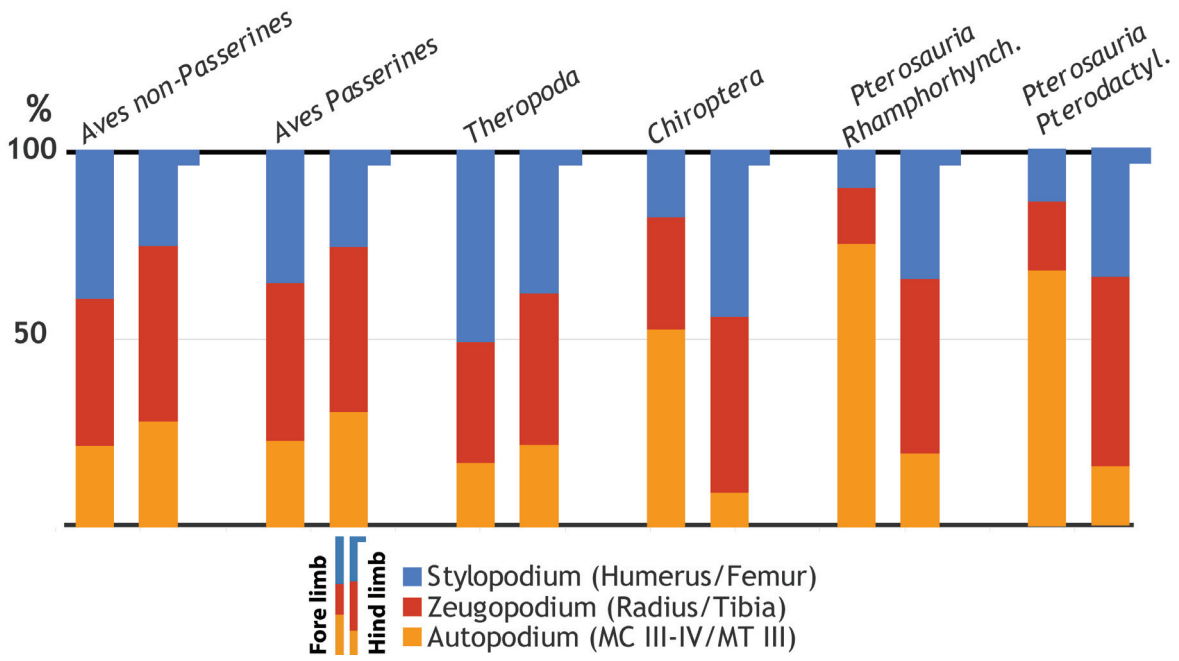

Figure 3.7 Groups centroids, in percentage, for fore and hind limb elements. Abbreviations: H - humerus, R/U – radius/ulna, MC - metacarpal III, F - femur, T - tíbia; MT metatarsal III.

Thus, the larger values of logratio variances appear when the autopodial elements are simultaneously present or when one of them, metacarpal or metatarsal, is compared to one of the opposite limb zeugopodium parts, i.e., radius-ulna vs. metatarsal or tibia vs. metacarpal.

Therefore, the logratio variance among the individuals of the total sample is bigger when one is comparing the fore limb autopodium against any hind limb bone, or the fore limb zeugopodium (radius) against the hind limb autopodium (metatarsal).

It should also be mentioned that the next higher logratio variances exist between: metatarsal and radius/ulna; metacarpal and humerus; metacarpal and femur.

	H	R/U	MC	F	T	MT	clr Var	% Var
H		.069	.633	.146	.142	.636	.041	**2.9**
R/U	-.129		.360	.191	.281	.974	.082	**5.9**
MC	.151	.281		.675	.991	2.184	.577	**41.7**
F	.457	.586	.306		.102	.628	.060	**4.3**
T	.006	.135	-.146	-.451		.281	.069	**5.0**
MT	.765	.895	.614	.309	.760		.553	**40.0**
Total variance = 1.382								

Table 3.7 – Variation array for Dyke et al. 2006 complete data set. Abbreviations: H - humerus; R/U – radius/ulna; MC – metacarpals III-IV; F – femur; T – tibia; MT – metatarsal III.

Taxonomical Individualized Variation

Analyzing the individualized taxa variation arrays results compiled in table 3.8, it was verified that the biggest logratio variances occur when autopodium parts are involved. Passerines show higher variability when the logratio engages the metatarsal and the radius/ulna or the metacarpal. Although the total variability of Passerines is lower than non-Passerines, the latter group reveals similar sources of variability in the same bone parts of Passerines.

Theropod dinosaurs expose higher logratio variances when one compares the parts radius/ulna against the metatarsal, the femur or the tibia. The source of variability in Theropoda is, therefore, from the fore limb zeugopodium against the hind limb bones.

The individual logratio variance matrix of Rhamphorhynchoidea reveals that most of the variability within its individuals arises from the logratios of the metacarpal and the femur or the tibia. Differently, Pterodactyloidea are more dissimilar among

individuals when the logratios of metatarsal and the metacarpal or the tibia are compared.

The variation array revealed similar logratio variances within both groups of bats, although with minor differences. The variability is higher when one compares the logratios of metatarsal against the femur or the tibia in both groups. However, in Microchiroptera the bigger source of variation among individuals comes from the logratio of both autopodial parts.

Taxa	Bone parts	logratio variances
	F-MT	.062
Megachiroptera	T-MT	.048
	H-MT	.043
	MC-MT	.055
Microchiroptera	T-MT	.052
	F-MT	.050
	R/U-MT	.216
Non-Passerines	MC-MT	.206
	H-MT	.200
	R/U-MT	.083
Passerines	MC-MT	.093
	H-MT	.056
	MC-MT	.097
Pterodactyloidea	F-MT	.084
	T-MT	.089
	T-MC	.175
Rhamphorhynchoidea	F-MC	.172
	H-MC	.108
	R/U-MT	.174
Theropoda	R/U-F	.141
	R/U-T	.115

Table 3.8 Three higher logratio variances between bone parts for Dyke et al. 2006 of individualized taxa data set. Abbreviations: Bones H - humerus; R/U – radius/ulna; MC – metacarpals III-IV; F – femur; T – tibia; MT – metatarsal III.

If one recalls the biplot of the *clr*-transformed space of the first two principal components for the complete sample - figure 3.9. a - it could be confirmed that the *clr*-autopodium elements are the most contributive parts for the greater part of the variance.

Considering the summary of *clr* variances of Aves and Theropoda bone parts - table 3.9 - all groups analyzed exhibit, in general, most of the *clr* variance in the autopodial bones and, depending on the group, in other appendicular elements.

Nevertheless, one notices that non-Passerines reveal the lowest relative variance in metacarpal.

One has detected that humerus is the least contributive element for the total theropods variance, showing a slightly smaller variance than Passerines - 6.4 and 6.9%, respectively, although in the referred birds group the least contributive element to the total variability is the femur.

The two bird groups display an important contribution of variance both on the radius/ulna and metatarsal bones. They could be distinguished chiefly by a more conservative pattern in the stylopodium among Passerines individuals proportions (humerus: 6.9% of total variance; femur: 6.7%), and a more dissimilar pattern among Passerines individuals, chiefly in metacarpal III proportion – 22.7%. Contrarily, non-Passerines exhibit more variance on the femur – 20.8% and are more conservative in metacarpal – 10.9 %.

Group		Fore limb						Hind limb						total *clr* variance
		clr H (var / %)		*clr* R/U (var / %)		*clr* MC (var / %)		*clr* F (var / %)		*clr* T (var / %)		*clr* MT (var / %)		
N=603	Non-Passe.	.036	**12.4**	.044	**15.1**	.032	**10.9**	.061	**20.8**	.025	**8.6**	.094	**32.2**	.291
N=97	Passe.	.006	**6.9**	.015	**16.6**	.020	**22.7**	.006	**6.7**	.010	**11**	.032	**36.1**	.088
N=14	Theropoda	.012	**6.4**	.052	**27.7**	.030	**15.8**	.038	**20.2**	.014	**7.2**	.043	**22.7**	.189

Table 3.9 *clr* variance and variance percentage for Dyke et al. 2006 Aves groups and Theropoda data set for the individual bone parts and within individual taxa. Abbreviations: var – variance; % - percentage of variance; H - humerus; R/U – radius/ulna; MC – metacarpals III-IV; F – femur; T – tibia; MT – metatarsal III; Rhampho. – Rhamphorhynchoidea; Pteroda. – Pterodactyloidea.

Birds' closest relatives, theropods, show a variance behavior similar to their descendants, except in femur, which presents, in theropods, bigger variance than metacarpal – 20.2 and 15.8%.

3.2.3 Aitchison Distances (A.D.) disparity metrics

Based on fore limb and hind limb proportions, the four main groups – birds, pterosaurs, theropods and bats - can easily be recognized in the built ternary diagram as described by Dyke et al. 2006 and McGowan and Dyke 2007.

Following the CDA methodology, the intragroups A.D. for both limbs means, standard deviation and maximum values were calculated - table 3.10 - and analyzed below.

Intragroups A.D. (fore/hind)	Mean (Fore/Hind)	SD (Fore/Hind)	Max. (Fore/Hind)
Non-passerines n=603	.148 / .263	.102 / .177	.861 / .913
Passerines n= 97	.110 / .149	.066 / .086	.315 / .431
Theropoda n= 14	.167 / .147	.057 / .102	.275 / .355
Chiroptera n=217	.117 / .178	.085 / .095	.817 / .513
Rhamphorhynch. n= 13	.248 / .199	.107 / .109	.420 / .393
Pterodactylo. n= 11	.123 / .200	.082 / .141	.308 / .503

Table 3.10 Intragroups A.D. mean, standard deviation (SD) and maximum (Max.). Abbreviations: Rhamphorhynch. – Rhamphorhynchoidea; Pterodactylo. – Pterodactyloidea; SD – standard deviation.

Intragroups A.D.

Fore limb

The most conservative group concerning fore limb proportions is Passerines, followed by Chiroptera, Pterodactyloidea and the non-Passerines, exhibiting A.D. means of 0.110, 0.117, 0.123 and 0.148, respectively. The most dissimilar group among individuals in fore limb proportions is Rhamphorhynchoidea, with an A.D. of 0.248, immediately followed by theropod dinosaurs.

These distinct A.D. indicate that both bird groups and bats reveal a more compact distribution in the fore limb morphospace, while pterosaur and theropod individuals are more spread in the same morphospace.

Comparing the two pterosaur groups, one detects that Rhamphorhynchoidea has an intragroup A.D. almost twice the one of Pterodactyloidea, thus revealing that rhamphorhynchoids has a fore limb disparity considerable larger than the pterodactyloids. This difference is an indicator of a bigger dissemination of rhamphorhynchoids pterosaurs in the fore limb morphospace. This discrepancy in fore

limb disparity could be interpreted as a result of distinct levels of phlygonetical groupings, since Rhamphorhynchoidea is not considered as a valid clade, i.e., one could be comparing two levels of classification when comparing Rhamphorhynchoidea and Pterodactyloidea.

Another potential interpretation for the distinct disparity indexes in pterosaurs could be that those results would suggest different functional performances among the two groups, that is, Pterodactyloidea fore limb morphology would have reached a functional evolutionary peak and, therefore, its disparity would have stabilized.

Although being analyzed for the fore limb A.D. as a single group, the Chiroptera sample integrates dozens of distinct species and exhibits lower A.D. than other groups with higher taxonomical diversity – non-Passerines. This fact reveals that bats present lower fore limb morphological disparity than non-Passerines, but higher morphological disparity than Passerines.

Theropoda small sample comprises, both in age and phylogeny, a significant range of its evolutionary history and, consequentially, one should be expecting that this group would present the higher disparity in the complete sample. This fact is partially verified, since only Rhamphorhynchoidea exhibit higher fore limb morphological disparity with a similar sample size.

These considerations on Theropoda fore limb disparity should be taken into account in future CDA studies that incorporate a bigger sample.

Hind limb

The groups that display smaller A.D. are theropod dinosaurs and Passerine birds, with values of 0.147 and 0.149, respectively. The groups more dissimilar among individuals in hind limb proportions are non-Passerine birds and both groups of

pterosaurs, with A.D. of 0.263, 0.200 and 0.199, for non-Passerines, Pterodactyloidea and Rhamphorhynchoidea, respectively.

Among pterosaurs hind limb almost identical A.D. was computed, implying that both groups of extinct flyers have similar disparity indexes. The two groups of birds reveal different A.D. for the hind limb, indicating a different exploration of the respective morphospace areas.

Bats reveals a hind limb dissimilarity index only higher than Passerines birds and theropod dinosaurs, groups that show equivalent A.D., although the dinosaur sample served merely as a comparative referential within the morphospace, not constituting an adequate sampling of that dinosaur taxa as stated in the introduction of this chapter.

Fore and Hind limbs

The A.D. of the hind limb are considerable bigger than the A.D. of the fore limb for all groups except theropods and rhamphorhynchoids pterosaurs. One, therefore, can state that the hind limb morphological disparity is in general bigger than the fore limb morphological disparity.

Intergroups A.D.

A.D. (fore/hind)	Non-Passerines	Passerines	Chiroptera	Rhamphorhy.	Pterodactyl.
Passerines	.140 / .099				
Chiroptera	1.216 / 1.198	1.122 / 1.273			
Rhamphorhy.	1.956 / .459	1.879 / 0.527	.781 / 0.746		
Pterodactyl.	1.674 / .640	1.601 / 0.721	.534 / 0.563	.286 / .219	
Theropoda	.412 / .503	.550 / 0.534	1.576 / 0.833	2.275 / .224	1.988 / 0.408

Table 3.11 Intergroups A.D. between all groups for fore limb and hind limb elements. Abbreviations: Rhamphorhy. – Rhamphorhynchoidea; Pterodactylo. – Pterodactyloidea.

Fore limb

The flying vertebrates in the Dyke et al. 2006 work were distinguished on basis of “visual-only” recognition and with absence of an adequate numeric quantification analysis of the constructed morphospace.

As understood in the CDA theoretical background, and materialized in figure 2.7, similar patterns of morphospace occupation or dispersion before centering could induce an incorrect inference of dispersion similarity. This fact is considerably amplified if one is analyzing “extreme” forms, that is to say, specimens that are closer to the borders of the morphospace. Equivalent incongruence could arise from the visual quantification of distances between individuals in the ternary morphospaces - recall figure 2.6.

In order to reduce some of the referred numerical limitations, the intergroups A.D. has been computed in order to evaluate the disparity between the groups in study - table 3.11.

Concerning the fore limb intergroups A.D., the most distant groups are Theropoda and the Rhamphorhynchoidea pterosaurs, with an A.D. of 2.275, followed by the Pterodactyloidea group, with an Aitchison Distance of 1.988 to Theropoda. This coefficient of dissimilarity is equivalent to the divergence quantified between Rhamphorhynchoidea and non-Passerine birds – A.D. 1.956. The closer groups to Chiroptera, i.e., with lower A.D., are the pterosaurs Pterodactyloidea and Rhamphorhynchoidea, with A.D. of 0.534 and 0.781, respectively.

The groups that reveal lower A.D. are Passerines and non-Passerines, closely followed by the two groups of pterosaurs, with A.D. of 0.140 and 0.286, respectively. The fore limb proportions indicate that theropods exhibit a lower A.D. to non-Passerines than to Passerines, although with comparable indexes – 0.412 and 0.550.

The clear difference between pterodactyloids and rhamphorhynchoids referred by Dyke et al. 2006 could not be confirmed by the intercentroid group Aitchison Distances. Fore limb intercentroid A.D. are smaller (half of A.D.) between the groups of

birds than between the pterosaurs. In the following section the differences among pterosaurs' limb proportions will be tested.

The comparison of Aitchison Distances between pterosaurs and birds reveal that Pterodactyloidea is closer to the extant flyers than Rhamphorhynchoidea, despite pterosaurs revealing considerable A.D.

The non-centered ternary diagram of fore limb proportions, depicted in figure 3.8, allows identifying specimens that are visually in the fringe of the morphospace and that could be easily classified as atypical.

Regarding birds morphospace occupation, one can observe a big dispersion and overlapping of specimens from both groups - figure 3.8, a and b. One can also notice a small group of nine non-Passerine specimens that are well separated from the rest of the bird species, which all belong to the families Apodidae and Trochilidae and that are classified as A.D. extreme values – see table 3.12, figure 3.9 and outliers description below.

The theropods occupy an area close to both bird groups and, despite its dispersion, are closer to non-Passerines than to Passerines. Despite being closely related to both birds and theropods among the clade Archosauria, pterosaurs occupy an extreme region of the morphospace and are closer to bats than to the referred archosaurians.

Within pterosaurs it could be observed that Pterodactyloidea fill a more restricted area of the morphospace than Rhamphorhynchoidea, which are more disperse and present extreme relative values mainly in metacarpal length.

The Chiroptera cluster reveals an identifiable trend in it's dispersion within the morphospace - detail in figure 3.8 c. This variation trend could be identified roughly as a variation in metacarpal relative length. It could be observed that some specimens fall out of the cluster, being one of them the most primitive bat - *Icaronycteris index*. Bats reveal a trend of variation somehow equivalent to pterosaurs and one could establish

the metacarpal variation range within the upper limit of more than 60% to the lower limit of less than 40% of *Taphozous flaviventris*. If one focuses on the bulk of the sample it could be stated that the variation ranges mainly from 50-60% in metacarpal to 25-35% in radius/ulna, with an almost constant humerus relative length of 15-20%. Microchiroptera cluster is less spread than the one of Megachiroptera.

Hind limb

The hind limb morphospace is perceptibly different than that of the fore limb, with most of the specimens occupying two major areas - figure 3.9. Despite some continuity in those two areas, one is occupied mostly by archosaurian specimens – theropods, birds and pterosaurs, being the other filled by bats. The limit region is mainly occupied by pterosaurs, and one can verify that theropods occupy a specific region of the hind limb morphospace.

One can also observe that, despite some overlapping, the groups of bats occupy distinct areas of the morphospace, being Megachiroptera individuals distributed in a broader area of the morphospace - figure 3.9, b and c. Thus, Microchiroptera exhibit a more compact morphospace occupation spanning relative length of femur from 34-57%, the tibia relative length from 36-53% and the metatarsal relative length from 5-14%. Megachiroptera relative length limits ranges from 37-45% of femur, 47-57% of tibia and 7-15% of metatarsal.

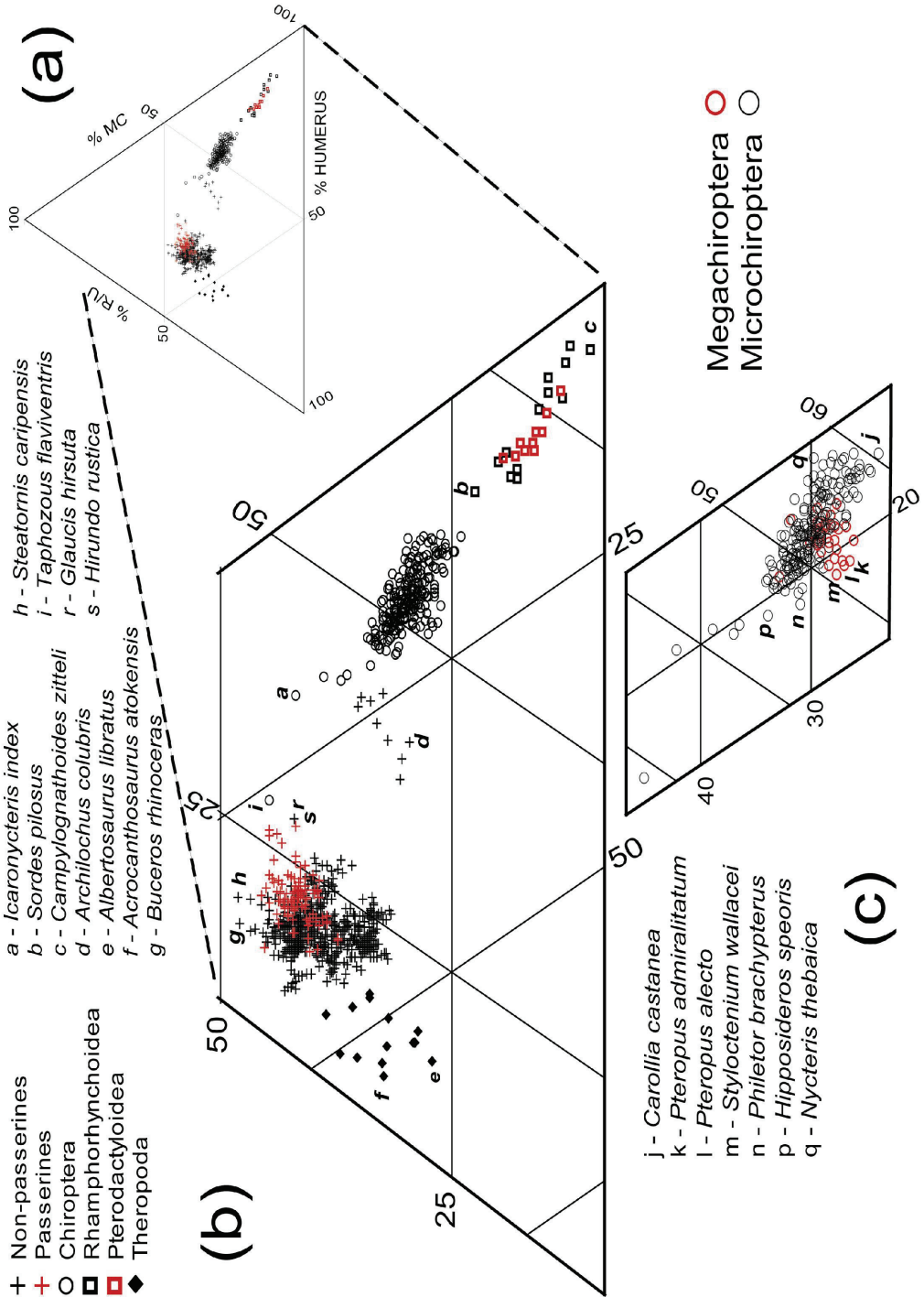

Figure 3.8 a) Empirical morphospace of fore limb parts of different flying vertebrates. b) All sample occupied area of morphospace. c) Chiroptera groups occupied area of morphospace. Specimens in the morphospace outskirt are identified.

The Aves groups morphospace area varies mainly along the femur axis, even if there is an observable variation along the other two axes. Comparing the two bird groups, one could state that Passerines morphospace is more compact than the one of non-Passerines. This fact could be, though, the consequence differences in groups' sample size.

Concerning pterosaurs, both groups occupy contiguous and overlapping morphospace areas but, despite that, one can distinguish that Rhamphorhynchoidea have lower percentages of tibia and higher percentages of metatarsal, implying that, for pterosaurs, femur's relative length is roughly constant.

The lowest value in hind limb intergroups A.D. was computed between Passerine and non-Passerine birds - 0.099, reflecting the close association in hind limb elements' proportions regarding those two sub-samples - table 3.11. This relationship between the two groups in hind limb elements' ratio is slightly inferior to the fore limb ratio (0.140), which could indicate that the differences in bone proportions observed are centered primarily in fore limb.

The disparity quantification here presented is the materialization of the functional discrepancies previously referred (Middleton and Gatesy 2000), more maneuverable fliers – Passerines vs. less maneuverable fliers – non-Passerines.

Despite being more related to birds than to pterosaurs, theropods reveal bigger A.D. to birds - non-Passerines 0.534 and Passerines 0.503 - than to pterosaurs - rhamphorhynchoids 0.224 and pterodactyloids 0.408. This close relationship in hind limb morphospace among phylogeneticaly distant groups could be interpreted as a result of functional constrains among flying vertebrates - birds and pterosaurs.

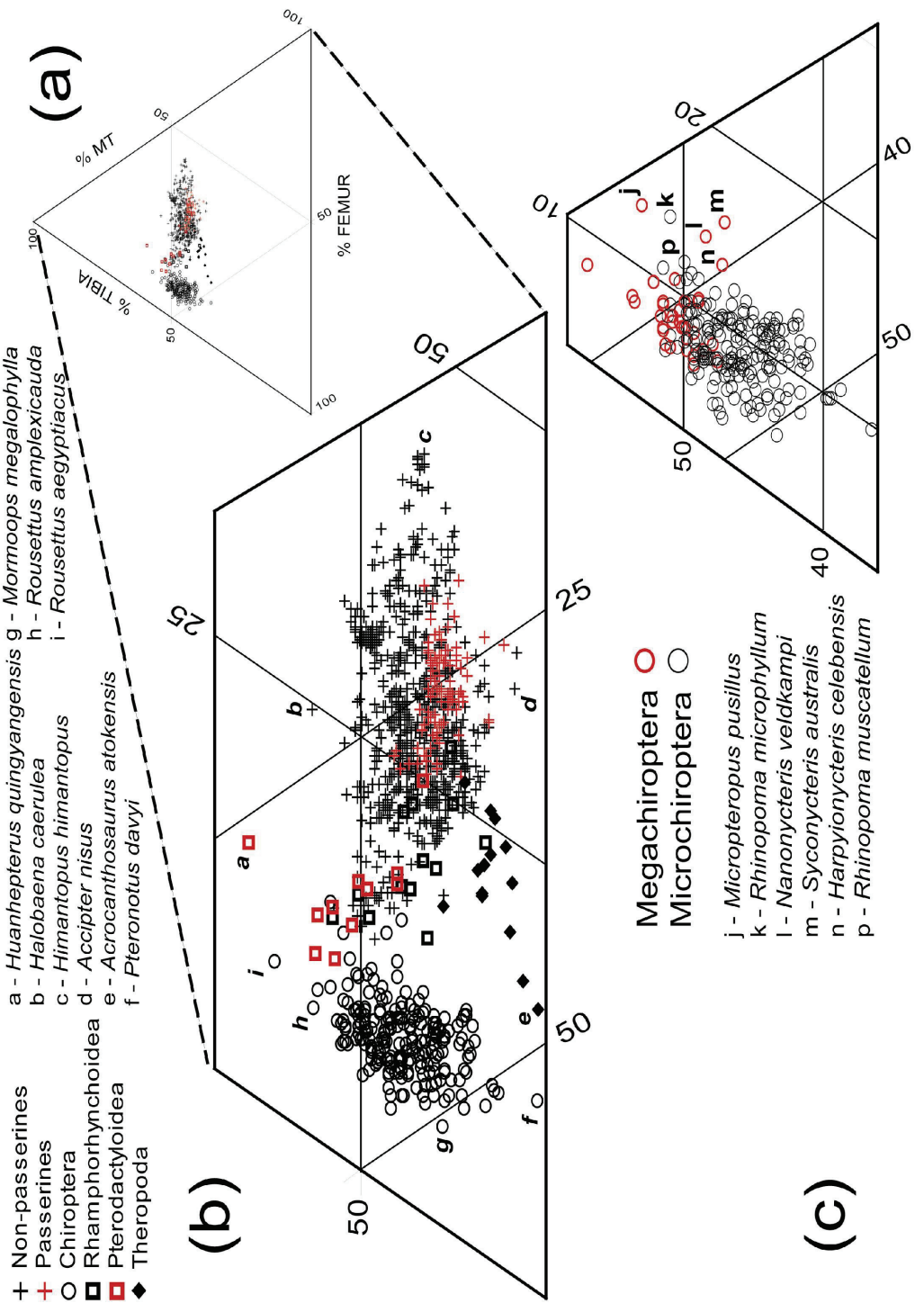

Figure 3.9 a) Empirical morphospace of hind limb elements of different flying vertebrates. b) All sample occupied area of morphospace. c) Chiroptera groups occupied morphospace. Specimens in the morphospace outskirt are identified.

Although not directly linked to flight[‡], could bird's hind limb be more conditioned by the function than by the phylogeny?

Observations on variation patterns in combined limbs

Notice that, in the empirical morphospaces, although both pterosaur groups are the closest ones to bats, Chiroptera show, both in fore and hind limb, smaller Aitchison Distances to Pterodactyloidea - 0.534/0.563 - than to Rhamphorhynchoidea pterosaurs - 0.781/ 0.746.

This consistent difference in proportions morphospaces patterning and distances of group centroids of pterosaurs to bats, both in fore and hind limbs, has never been quantified.

Despite the big difference between Theropoda and Pterosauria in forelimb intercentroid A.D. - 2.275 for Rhamphorhynchoidea and 1.988 for Pterodactyloidea - the A.D. values for hind limb are considerably reduced - 0.224 for Rhamphorhynchoidea and 0.408 for Pterodactyloidea. These facts could be explained by the big functional differences in hind limb in those two groups. The forelimb, oppositely, is more related in pterosaurs and theropods proportions.

The clear difference referred between pterodactyloids and rhamphorhynchoids (Dyke et al. 2006) could not be confirmed by the intercentroid group A.D. The A.D. of fore limb and hind limb are considerably smaller between the two groups of birds than between the pterosaur's groups.

Outliers A.D. intradistances

The box-plots of the different clades intragroups A.D. has been computed - figure 3.10. One has decided to perform this calculation in order to identify which species are more dissimilar within each group. The disparity index used, A.D., inform us

[‡] This is more evident in birds, since there are evidences of membrane attachment in the hind limb of pterosaurs, originating this fact an effective contribution of hind limb to active flight.

on the most distant species to its limb proportions centroid. This biological information is relevant since those quantified dissimilarities could be interpreted under ecological and/or functional constrains and allow understanding part of the evolutionary history of the analyzed groups.

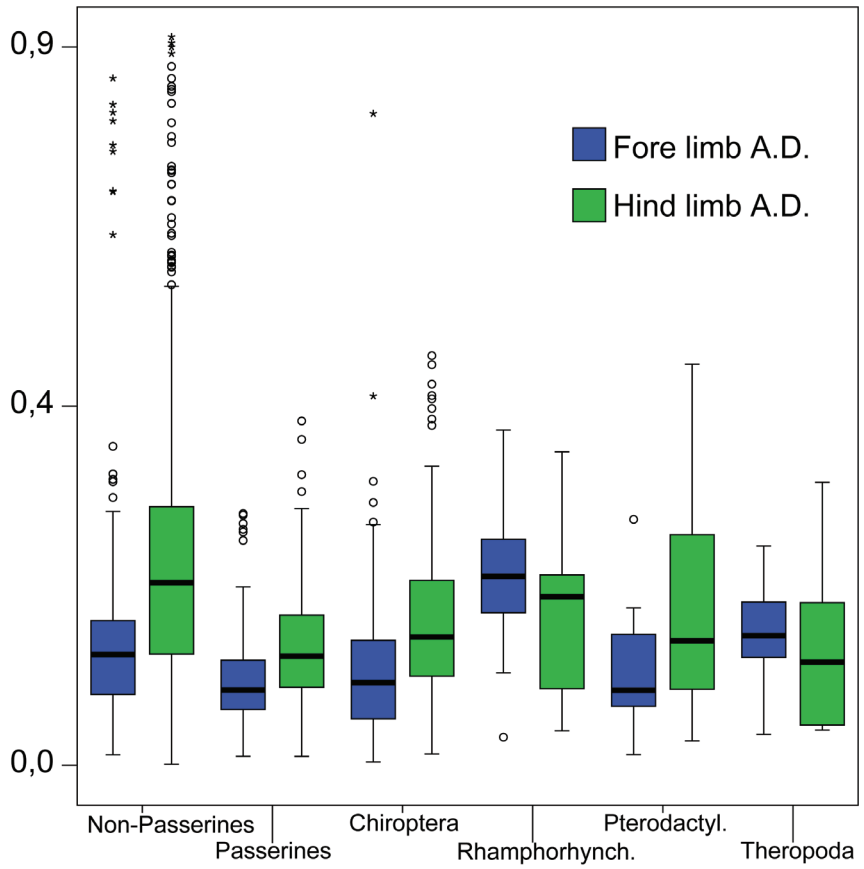

Figure 3.10 Box-plots of intragroups A.D. The A.D. for chiroptera was computed for the non-discriminated sample, i.e., considering Megachiroptera and Microchiroptera as a single group. Outliers species indicated in Table 3.12.

Non-Passerines has the highest number of A.D. outliers in the sample followed by Passerines and Chiroptera - figure 3.10. The two pterosaur groups show only one outlier each and both in fore limb. Theropoda does not have any outlier.

It could also be detected a substantially higher number of outliers in the hind limb than in the fore limb in non-Passerines and bats. This trend is not verified in Passerines which exhibit bigger number of fore limb proportions outliers.

Outliers and Extreme Values[1]	Limb	Non-Passerines	Passerines	Chiroptera	Rhamphorhynch.	Pterodactyl.
Intragroups A.D.	Fore	**Apodiformes** **Apodidae** *Apus affinis*[1](aerial) *Apus apus*[1](aerial) *Chaetura pelagica*[1](aerial) **Trochilidae** Archilochus colubris[1](aerial; trees) Glaucis hirsuta[1](aerial; trees) Patagona gigas[1](aerial; trees) **Procellariiformes** *Diomedea exulans* (aerial;swimmer) *Diomedea irrorata* (aerial;swimmer)	**Hirundinidae** *Delichon urbica* *Hirundo rustica* *Petrochelidon pyrrhonota* *Riparia riparia* **Laniidae** Lanius excubitor	**Megachiroptera** *Rhinopoma muscatellum* *Rhinopoma microphyllum* *Rhinopoma hardwickei* *Taphozous flaviventris*[1] **Microchiroptera** *Icaronycteris index*[1]	*R. intermedius*[+]	*Pteranodon sp.*
	Hind	**Psittaciformes** *Amazona farinosa* (trees) *Cacatua galerita* (trees) *Calyptorhynchus magnificus* (trees) *Pionus senilis* (trees) **Coraciiformes** *Megaceryle alcyon* (aerial) **Sphenisciformes** *Eudyptes crestatus* (ground;swimmers) **Ciconiiformes** **Fregatidae** *Fregata aquila* (swimmer) *Fregata sp.* (swimmer) **Recurvirostridae** *Himantopus himantopus*[1] (waders) *Himantopus leucocephalus* (waders) *Himantopus mexicanus* (waders) **Ciconiidae** *Xenorhynchus asiaticus* **Falconiformes** **Accipitridae** *Sagittarius serpentarius* (ground) **Cathartidae** *Vultur gryphus*[1] (ground) **Procellariiformes** *Pelagodroma marina* **Phoenicopteriformes** *Phoenicopterus antiquorum*[1] (waders) *Phoenicopterus rubber*[1](waders)	**Tyrannidae** *Muscigralla brevicauda* **Reguliidae** *Regulus regulus* **Acanthisittidae** *Xenicus longipes*	**Megachiroptera** *Micropteropus pusillus* *Nanonycteris veldkampi* *Syconycteris australis* **Microchiroptera** *Barbastella barbastella* *Cheiromeles torquatus* *Nycteris thebaica* *Plecotus austriacus* *Rhinopoma microphyllum*		

Table 3.12 Fore and hind limb A.D. outliers and extreme values for sample groups. Between parentheses are the habitat affiliations proposed by Zeffer et al. (2003) for different bird species. Bird species which does not have habitat affiliation attributed were not analyzed by Zeffer et al. (2003). Birds classifications followed Myers et al. 2008. 1 - extreme values; + - lower outlier (*Rhamphorhynchus intermedius*).

One have separated the Non-Passerines outliers in the corresponding Orders and Families, in the cases which for the same Order there are more than one Family, in order to evaluate a possible phylogenetical signal for the A.D. atypicality index.

The classification of Myers et al. (2008) has been adopted which is coherent, at least for the outliers, to the recent phylogenetical nomenclature of Livezey and Zusi (2007).

Regarding non-Passerines fore limb outliers they are from two Orders – Apodiformes and Procellariiformes; concerning the hind limb they belong to seven

orders: Psittaciformes, Coraciiformes, Sphenisciformes, Ciconiiformes, Procellariiformes, Phoenicopteriformes and Falconiformes.

One has identified the habitat groups[§] of the non-Passerines outliers, and following the habitat affiliations proposed by Zeffer *et al*. (2003), in order to evaluate a possible ecological signal in the disparity atypical identification. On the hind limb outliers habitat affiliations, it could be detected that they mainly integrate waders, swimmers and ground species. Thus, the most disparate species on hind limb A.D. are mainly species that depend on the hind limb locomotor capabilities to its ecological success. The disparate positioning in the hind limb morphospace could be therefore explained by the hind limb morphological specializations intimately linked to habitat preferences.

It should be mentioned that earliest known bat fossil *Icaronycteris index* is considered to have equivalent forelimb digits proportions as extant bats (Sears et al. 2006). In this work *I. index* is classified to be an outlier in fore limb bones proportions.

3.2.4 Statistical Tests

A.D. ANOVA

In the present work it has been assumed that A.D. should be interpreted as a limb elements proportions disparity index. In order to compare intragroups fore limb A.D. means one has performed the t-test which confirmed that there are significant differences between the two groups A.D. means of pterosaurs fore limbs (t= 3.157, P=0.005). The same test did not confirm significant differences in the hind limb A.D. means among both groups of pterosaurs (t= -0.012, P=0.990).

[§] "Aerial birds include species with a passive use of the legs, for example, mostly during perching or just sitting on the ground. Ground species include species that predominantly use the legs for terrestrial locomotion, such as walking, running or hopping. Tree species include birds that predominantly forage in trees or bushes. Swimming species predominantly use the legs for swimming. Wading species forage by wading in water." adapted from Zeffer *et al*. (2003, p.462)

These results indicate that Rhamphorhynchoidea and Pterodactyloidea reveal different disparity indexes, i.e. A.D., in fore limb proportions. Rhamphorhynchoidea exhibit, therefore, a larger morphospace occupied area than Pterodactyloidea.

Therefore, it could be said that the two pterosaur sub-groups present different fore limb morphospace occupation patterns. Oppositely, both pterosaur groups reveal similar hind limb disparity indices, i.e., they present a similar pattern of hind limb morphospace occupation.

These results contradicts Dyke et al. 2006 that, despite recognizing different patterns of morphospace occupation for the two pterosaur groups, stated that there is no marked difference between Rhamphorhynchoidea and Pterodactyloidea fore limb proportions.

ilr MANOVA

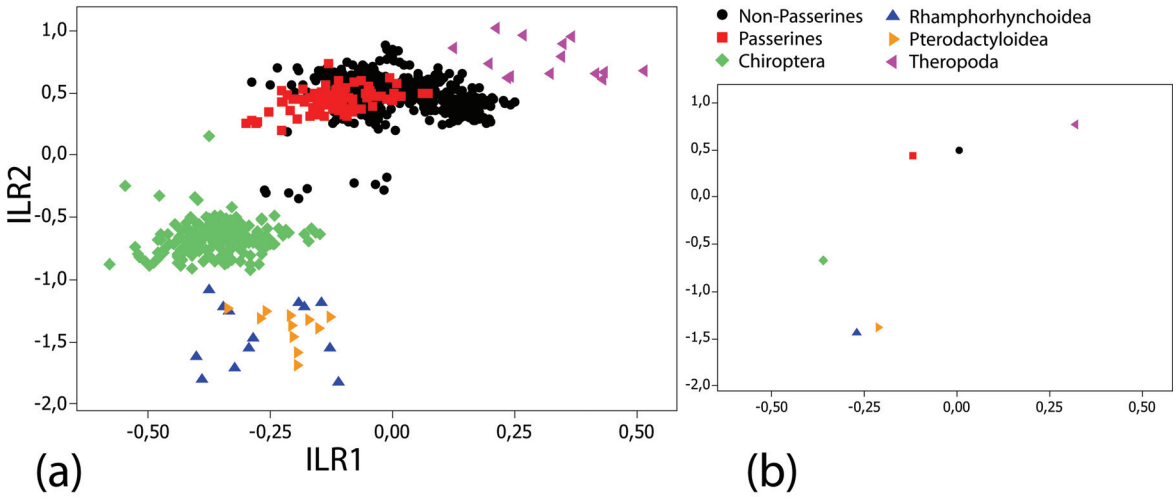

Figure 3.11 a) *ilr*-coordinates plot of fore limb proportions of all sample; b) *ilr* -coordinates plot of fore limb group means proportions.

Fore limb

As stated in the CDA introductory section one will use the *ilr* in the MANOVA's tests instead of *clr* since *clr* covariance matrix is, among other peculiarities, singular.

MANOVA indicated highly significant differences in fore limb elements proportions among the six groups means - Wilks' lambda = 0.035, F[10,1896] =822.365, P < 0.001.

When one compares the fore limb means of non-Passerines and Passerines there is still significant differences between group means - Wilks' lambda = 0.819, F[2,697] =77.196, P < 0.001. Detailed analysis indicated that there are significant differences whatever logratio of parts chosen, i.e., the two groups of birds are different in fore limb proportions for every logratio that one chooses to analyze.

Comparing the two groups of pterosaurs, MANOVA indicated no significant differences among the group means – Wilks' lambda = 0.875, F[2,21] =1.496, P = 0.247.

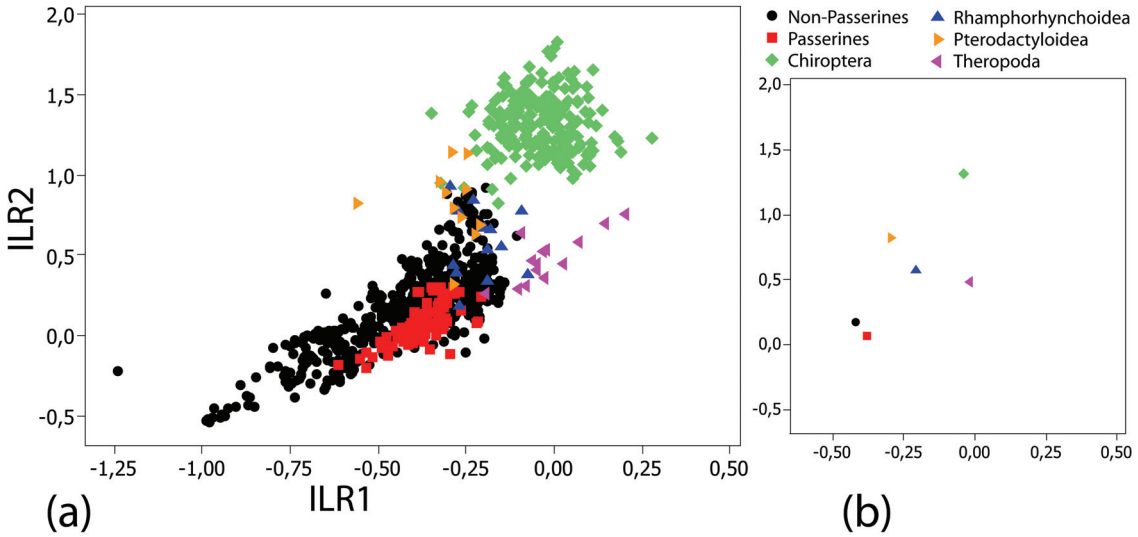

Figure 3.12 a) *ilr*-coordinates plot of hind limb proportions of all sample; b) *ilr*-coordinates plot of hind limb proportions group means.

Hind limb

The MANOVA analysis of the *ilr*-coordinates indicated highly significant differences in hind limb elements proportions among the six groups means - Wilks' lambda =0.147, F[10,1896] =305.032, P < 0.001.

When one compares the hind limb means of Non-Passerines and Passerines there is still significant differences between group means - Wilks' lambda =0.885, F[2,697] =45.172, P< 0.001. Detailed analysis indicated that there are significant differences between the two groups of birds whatever logratio of parts is chosen to analyze.

Analyzing the two groups of pterosaurs, MANOVA indicated significant differences among the hind limb groups means – Wilks' lambda =0.633, F[2,21] =6.096, P=0.008. Detailed analysis indicated that there are significant differences between the two groups of pterosaurs whatever logratio of parts is chosen to analyze.

Chiroptera - MANOVA

In order to evaluate the existence of differences in fore limb proportions among the two groups of Chiroptera, one has performed MANOVA tests in *ilr* coordinates.

The MANOVA analysis of the *ilr*-coordinates indicated highly significant differences in fore limb elements proportions among the two group means - Wilks' lambda =0,814, F[2,214] =24,452, P < 0.001.

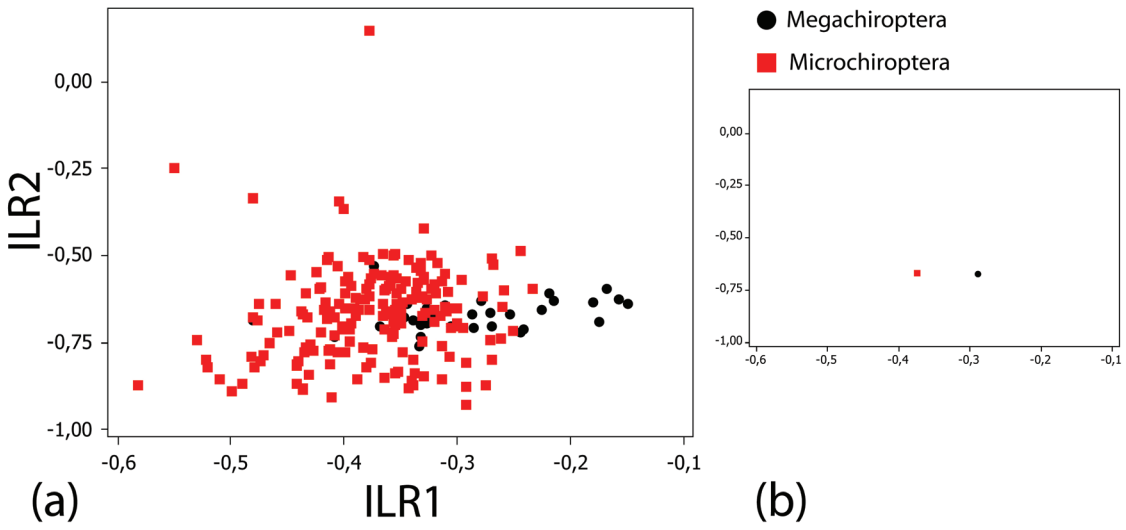

Figure 3.13 a) *ilr*-coordinates plot of fore limb proportions of Chiroptera sample; b) *ilr*-coordinates plot of fore limb proportions group means.

The MANOVA analysis of the *ilr*-coordinates indicated highly significant differences in hind limb element proportions among the two group means - Wilks' lambda =0,724, F[2,214] =40,719, P < 0.001.

If one compares the graphs of the *ilr*-coordinates of group means of fore and hind limb proportions, it could be suggested that the main differences between groups are due mainly to *ilr*1, i.e., the ratios humerus-radius and femur-tibia, respectively for fore and hind limb, and not due to *ilr*2 – figures 3.13 and 3.14.

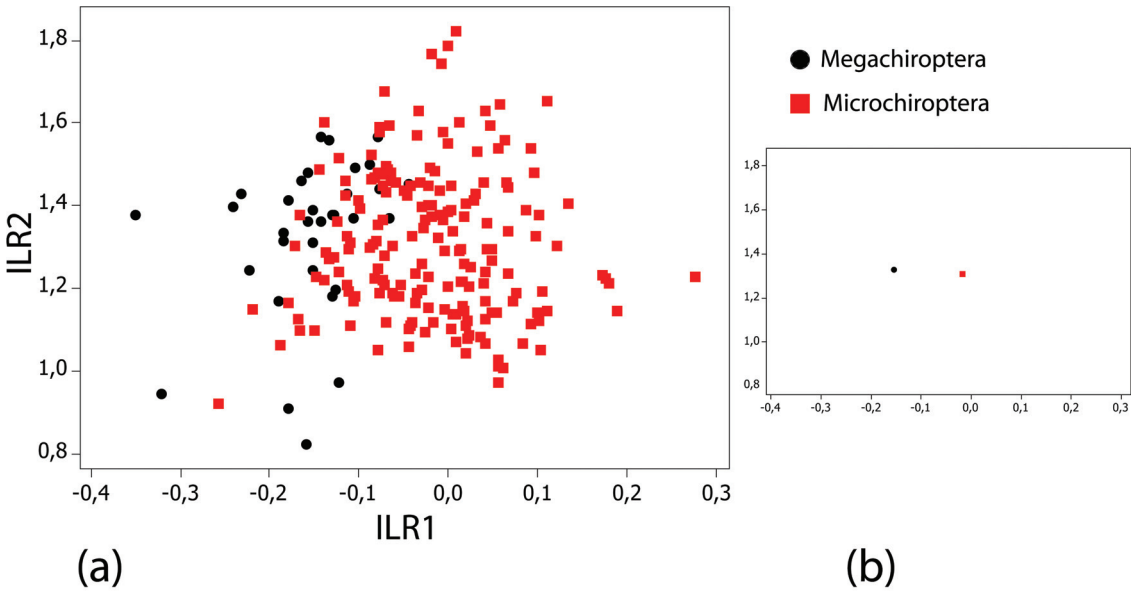

Figure 3.14 a) *ilr*-coordinates plot of hind limb proportions of Chiroptera sample; b) *ilr*-coordinates plot of hind limb proportions group means.

Analyzing the biplots and both variation arrays for Megachiroptera and Microchiroptera, depicted in figures 3.15 and 3.16 and table 3.13, which allow exploring the relative variation between the six parts of bats, one observes that the hind limb elements of Megachiroptera reveals higher variability than the homologous elements of Microchiroptera – 59.4 *vs* 54.9%. This implies that the fore limb elements of Microchiroptera are more disparate than the equivalent limb of Megachiroptera.

	Megachiroptera (n=33)								Microchiroptera (n=184)							
	H	**R/U**	**MC**	**F**	**T**	**MT**	***clr* var**	**% var**	**H**	**R/U**	**MC**	**F**	**T**	**MT**	***clr* var**	**% var**
H		.016	.012	.014	.013	.044	.008	**11.9**		.008	.031	.024	.034	.045	.012	**14.3**
R/U	-.418		.019	.026	.025	.041	.011	**15.5**	-.529		.027	.015	.023	.039	.009	**11.2**
MC	-1.015	-.598		.028	.016	.034	.009	**13.2**	-1.084	-.555		.031	.049	.055	.016	**19.6**
F	.671	1.088	1.686		.012	.064	.012	**17.5**	.389	.917	1.473		.014	.050	.011	**13.4**
T	.461	.879	1.477	-.210		.048	.009	**13.8**	.364	.892	1.448	-.025		.052	.014	**17.2**
MT	2.196	2.613	3.211	1.525	1.734		.019	**28.1**	1.977	2.505	3.061	1.588	1.613		.020	**24.3**
	Total variance = 0.0686								**Total variance = 0.0828**							

Table 3.13 Variation arrays for Dyke et al. 2006 Chiroptera data set. The Chiroptera data set was divided accordingly to two-sub orders: Megachiroptera and Microchiroptera. Abbreviations: H - humerus; R/U – radius/ulna; MC – metacarpal III; F – femur; T – tibia; MT – metatarsal III.

The *clr*-femur in Megachiroptera is more disparate than in Microchiroptera – 17.5% vs. 13.4%. Similar high variability could be identified for the *clr*-metatarsal of Megachiroptera, exhibiting this bone almost half of the total variability of this sub-order – 28.1%, contrary of what is quantified for Microchiroptera in which the metatarsal contributes with 24.3% for the total variability.

The metacarpal is the second most uneven element among Microchiroptera individuals and with higher relative variability than in Megachiroptera – 19.6% *vs* 13.2%. Also the humerus is somewhat more variable in Microchiroptera than in Megachiroptera – 14.3% *vs* 11.9%. This trend is not observable in the fore limb zeugopodium element – the radius/ulna, which is present in a more conservative proportion in Microchiroptera than in Megachiroptera – 11.2% vs. 15.5%.

If one now focuses the comparison on the homologous elements of both groups, it could be detected that the autopodium components – metacarpal and metatarsal – exhibit almost half of the total variability in both groups of bats, although being slightly larger in Microchiroptera – 43.8 % vs. 41.2 %.

***clr* variance - %**	Fore limb	Hind limb	stylopodium (H+F)	zeugopodium (R/U+T)	autopodium (MC+MT)
Non-Passerines	38.4	61.6	33.2	23.7	43.1
Passerines	46.2	53.8	13.6	27.6	58.8
Theropoda	49.9	50.1	26.6	34.9	38.5
Megachiroptera	40.6	59.4	29.4	29.3	41.2
Microchiroptera	45.1	54.9	27.7	24.7	43.8
Rhamphorhynchoidea	53.2	46.8	26.3	31.4	42.3
Pterodactyloidea	40.8	59.2	26.7	26.8	46.0

Table 3.14 Sums of percentages of *clr* variance of sample groups, between limbs and between homologous elements. Abbreviations: **H** - humerus, **R/U** – radius/ulna, **MC** - metacarpal III, **F** - femur, **T** - tibia and **MT** - metatarsal III.

The topological intermediate group of bones – radius and tibia – show different relative variability among the two groups but in Microchiroptera and Megachiroptera the zeugopodium is the least most important origin of variability among individuals – 24.7 % vs. 29.3% of the quantified variance. In Megachiroptera this module of bones reveal almost identical variability to the stylopodium elements – humerus and femur. In Microchiroptera the most proximal group of bones is more variable than the intermediate group; the combined humerus and femur variances reveal higher variance than the radius and tibia combined variances - 27.7 % vs. 24.7 %.

Chiroptera

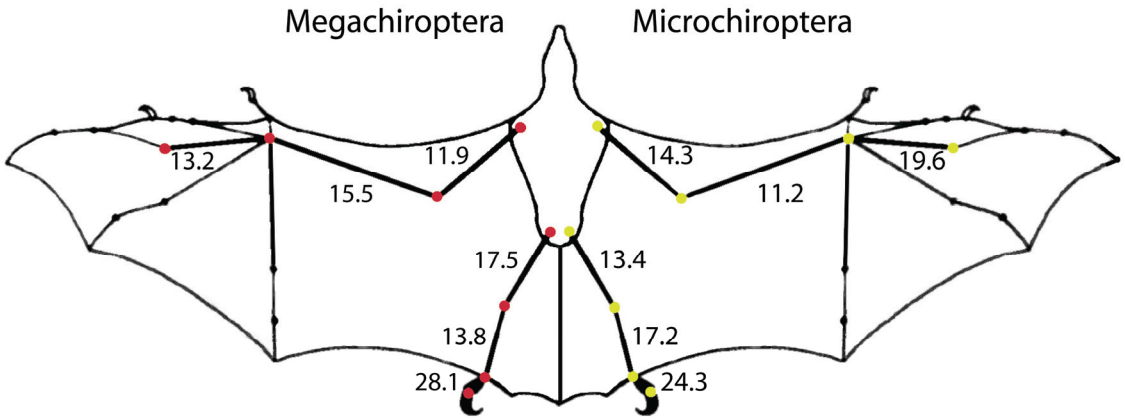

Figure 3.15 Megachiroptera and Microchiroptera bone proportions variability expressed as percentages of *clr* variance. Generic bat silhouette adapted from Schutt and Simmons 1998, fig. 9-c.

Figure 3.15 resumes the bone parts variability in both Chiroptera groups and it could be stated that:

- in bats the fore limb is more conservative than the hind limb;
- Microchiroptera demonstrates higher fore limb proportions variability than Megachiroptera;
- in both groups the most variable bone is the metatarsal being this structure more variable in Megachiroptera than in Microchiroptera;
- Megachiroptera reveals higher hind limb variability than Microchiroptera;
- in Microchiroptera the variability steadily increases distally in the fore limb;

As introduced in the previous chapter section 2.2.7 and concretized in biplots for the non-discriminated sample - figure 2.9 a - one observes that the PC1 is controlled mainly by the autopodial elements and that tibia and femur reveal an evident control on PC2. One also notes that the influence of bone parts is reducing distally to proximally. The biplot analyzed in 2.10 b results from a comparison of the two groups of pterosaurs and the results analyzed below corroborate the results of the *clr* variance - table 3.16.

One will now focus on the biplots of the two groups of bats firstly in a combined analysis and then separately - figures 3.15 and 3.16. The biplot of Chiroptera six parts allows stating that the two main axes which explain most of the variance are very similar in importance – 38% and 30%, and therefore the variables associated with

each axis explain equivalently the variability. PC1 is mainly influenced by two bone parts, metatarsal and, at a minor scale, by femur, despite the fact that the other bones also contribute to this axis, with reduced influences. Metatarsal has the longest ray which exposes its large influence in the total variability among individuals being followed, in importance, by the metacarpal and tibia.

PC2 is mostly influenced by metacarpal and tibia, although, as stated to PC1, other bones explain the variability of the second axis. We should mention that most of the total variability among bat individuals is due to hind limb bone proportions – compare these results with *clr* variance analysis.

It is worth to mention that fore limb logcentered variables are associated in the same quadrant and are related to PC2. The two groups of bats exhibit a considerable number of specimens spread along both axis but one can roughly state that Megachiroptera is less disperse along PC1 than in PC2, being the former coupled chiefly with metatarsal, as stated above.

Individual biplots of the two groups of bats allowed us to identify diverse atypical outliers[**], namely four in Megachiroptera and ten in Microchiroptera with no evident taxonomic signal since in ten specimens there are seven families represented in the Microchiroptera outliers - figures 3.16 and 3.17 a and b. Megachiroptera is constituted by single Family sub-order and therefore no taxonomic lower-level signal is identifiable.

Examining the two individualized biplots one detects that the Microchiroptera results are almost identical to the non-discriminated biplot, with the slight difference of the relative importance of the variable femur. One interprets that resemblance as a result of the big difference in sample size of the two bat sub-orders[††] and which is statistically constraining the result. Since the combined biplot was described already and the differences towards Microchiroptera are minimal, one shall now focus on the

[**] The outliers are not represented in the figures 3.16 and 3.17 for better clarity of the results.

Megachiroptera biplots - figure 3.17 b. For similar reasoning, the comparison of the biplots of bats two sub-orders will be performed at the end of this chapter.

As stated above the only clear difference between the biplots of the combined sample and the Michochiroptera is the relative importance of the femur on the total variability being larger in Microchiroptera than in the combined sample. One interprets this fact due to the strong influence of the femur on Megachiroptera which is conditioning the cited femur differences.

As expressed for the combined sample, Microchiroptera reveal similar percentages of explained variance for the first two axes – 39% and 32%, respectively. The PC1 is mainly controlled by the metatarsal and with minor influences of the femur and tibia. PC2 is determined mainly by metacarpal and femur with minor influences of humerus and radius.

Megachiroptera biplot is distinct from the equivalent of Microchiroptera since the percentage of explained variance for the first axis is more than three times the explained variance of the second axis, and the combined variances explains 83%. In Megachiroptera sample PC1 is mainly influenced by metatarsal, which is the most relevant ray, followed by the logcentered variables femur and tibia. These hind limb bones are practically collinear and their vertices are very close implying that the femur and tibia parts have an almost constant proportion (0.811) - recall chapter 2, sections 2.2.5 and 2.2.7. Similarly, an almost constant proportion of femur relative to tibia, i.e. they reveal logratios variance close to zero, has already been observed and quantified - 0.9467 - for both groups of pterosaurs – figure 2.10 b.

[††] Megachiroptera: n=33; Microchiroptera: n=184

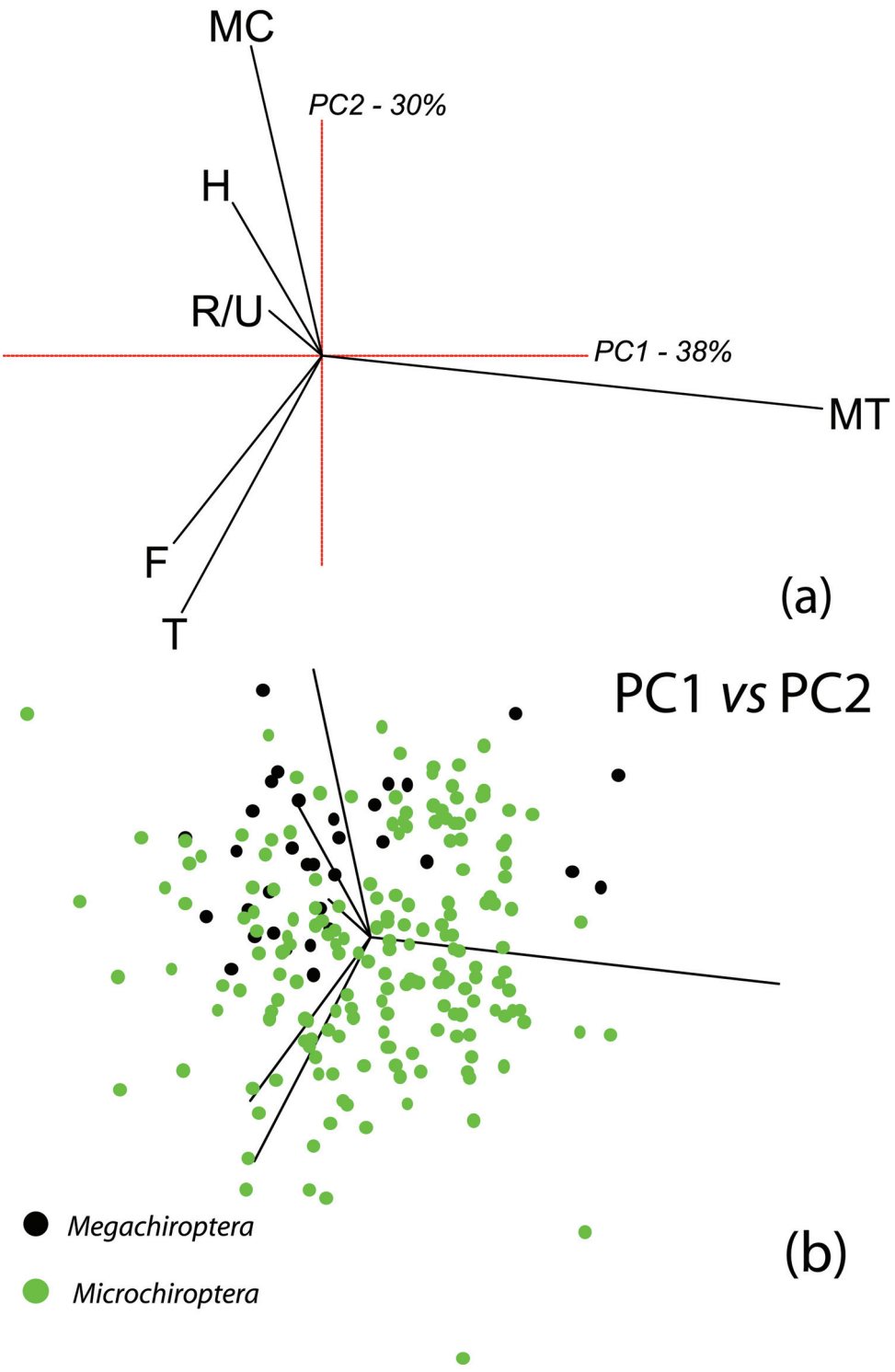

Figure 3.16 a) Biplot of the *clr*-transformed space of the first two principal components (PC1 *vs* PC2) of Chiroptera, six limb parts (Dyke et al. 2006 database; see 3.2. for details). First Principal Component (38%), Second Principal Component (30%), Third Principal Component (18%), Fourth Principal Component (10%), Fifth Principal Component (4%). b) Biplot of the *clr*-transformed space with all specimens of bats. Outliers (not represented in the figure but identified in the biplot analysis) - *Cheiromeles torquatus*, *Icaronycteris index*, *Micropteropus pusillus*, *Nycteris thebaica*, *Pteronotus davyi*, *Pteropus alecto*, *Rhinopoma microphyllum*, *Rhinopoma muscatellum*, *Rousettus aegyptiacus*, *Taphozous flaviventris*, *Tonatia bidens*. Abbreviations: H - humerus; R/U – radius/ulna; MC - metacarpal III; F - femur; T - tíbia; MT - metatarsal III.

The importance of the metacarpal on the total variability of Megachiroptera is somewhat equivalent to the radius and considerable smaller than in Microchiroptera. This implies that the fore limb bigger digit present a more conservative pattern in Megachiroptera than in Microchiroptera. Recall, additionally, the variation matrix for both groups of bats in which the *clr* variance of the metacarpal in Megachiroptera is 13.2 % vs. 19.6 % in Microchiroptera - table 3.13.

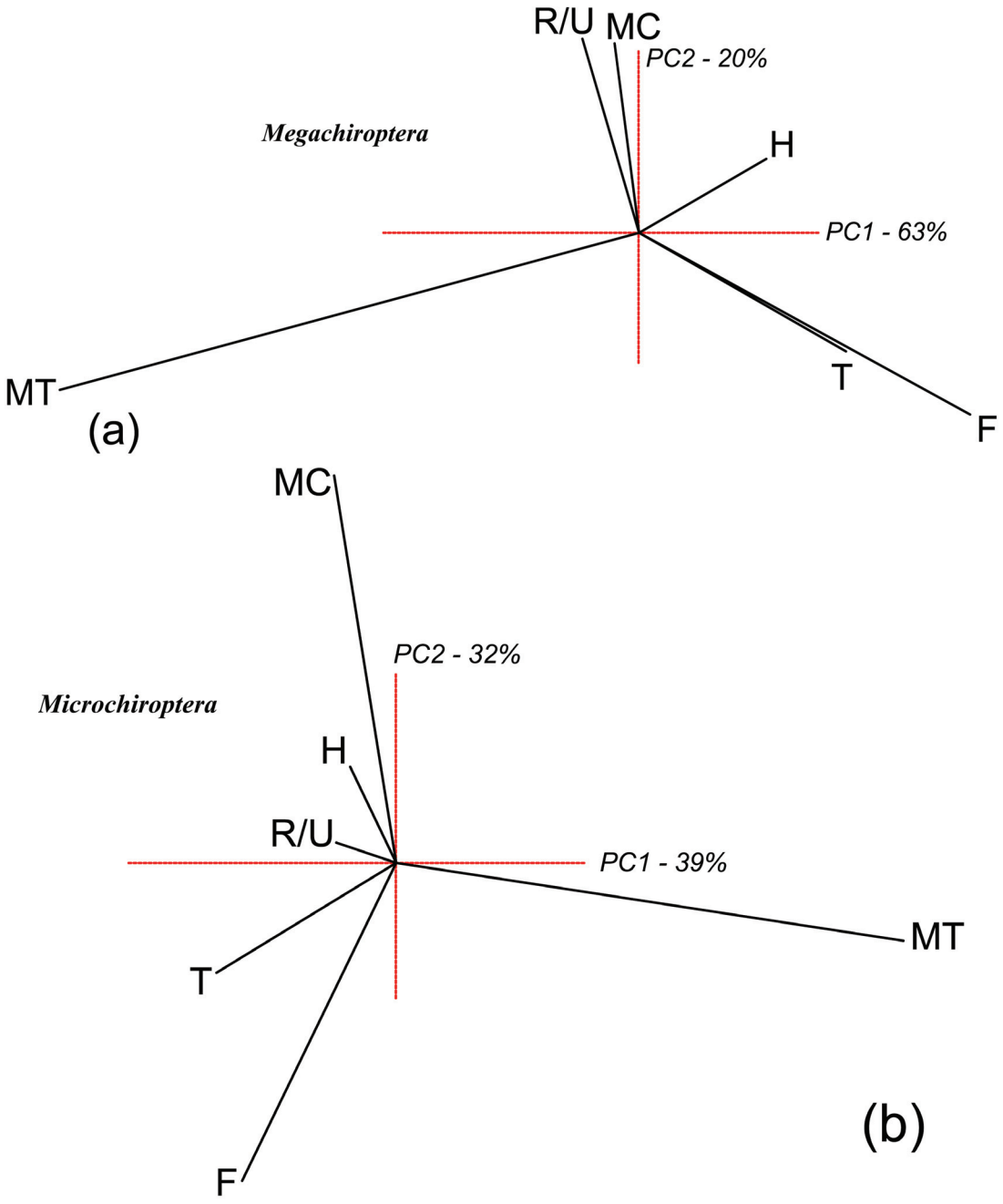

Figure 3.17 a) Biplot of the *clr*-transformed space of the first two principal components (PC1 vs. PC2) of Megachiroptera sub-sample, six limb parts. First Principal Component (63%), Second Principal Component (20%), Third Principal Component (9%), Fourth Principal Component (7%), Fifth Principal Component (3%). Outliers (not represented in the figure but identified in the biplot analysis) - *Rousettus aegyptiacus*, *Rousettus amplexicaudatus*, *Micropteropus pusillus* and *Sphaerias blanfordi*. b) Biplot of the *clr*-transformed space of the first two principal components (PC1 vs PC2) of Microchiroptera sub-sample, six limb parts. First Principal Component (39%), Second Principal Component (32%), Third Principal Component (19%), Fourth Principal Component (6%), Fifth Principal Component (4%). Outliers (not represented in the figure but identified in the biplot analysis) - *Icaronycteris index*, *Rhinopoma microphyllum*, *Rhinopoma muscatellum*, *Taphozous flaviventris*, *Nycteris thebaica*, *Megaderma spasma*, *Pteronotus davyi*, *Tonatia bidens*, *Amorphochilus schnablii* and *Cheiromeles torquatus*. Abbreviations: H - humerus; R/U – radius/ulna; MC - metacarpal III; F - femur; T - tíbia; MT metatarsal III. Dyke et al. 2006 database; see 3.2. for details.

Pterosauria

Pterosaurs, disregard showing similar trends to other groups, reveal some variability particularities among the individual bones - table 3.15. Rhamphorhynchoidea disclose most of the *clr* variance in metacarpal IV, tibia and femur, in decreasing order. Pterodactyloidea reveal the highest variance in metatarsal III but one could also identify high levels of variability in metacarpal IV and tibia.

Analyzing the variation arrays for the two groups of pterosaurs one observes that most of the bone parts reveal almost identical variability percentages except for the radius, the metacarpal IV and the metatarsal III. The metacarpal IV is far more conservative in Pterodactyloidea than in Rhamphorhynchoidea (19.4% vs. 28.0%) but pterodactyloids reveal bigger variability in the metatarsal III - 26.6% vs. 14.3. The radius influence on the total variability is bigger in the Rhamphorhynchoidea.

Therefore and in terms of percentages of variability, one could state that the two groups of pterosaurs could be recognized through the more disparate metatarsal proportion in Pterodactyloidea, while Rhamphorhynchoidea reveal a higher variability in metacarpal IV and radius proportions.

Comparing pterosaurs combined variability of homologous bones one detects that limb proximal parts – humerus and femur – present a stable pattern of variability within both groups. Variability increases distally and is higher in Rhamphorhynchoidea than in Pterodactyloidea. This variability increase trend among distal bones shows that Pterodactyloidea present the most dissimilar autopodial elements – total combined percentage of *clr* variance of metacarpal and metatarsal is 46.0 vs. 42.3 in Rhamphorhynchoidea.

Comparing fore and hind limb elements variability one notices that Pterodactyloidea has hind limb proportions far more diverse (59.2%) than Rhamphorhynchoidea (46.8%). Consequently, the pterodactyloids reveal a more comparative variability pattern among the two limbs.

Analyzing in detail each individual part one observes an almost identical variability among the humerus and radius/ulna of Pterodactyloidea. A similar variability pattern is not verified in those elements of Rhamphorhynchoidea since the radius/ulna proportion presents bigger variability than the variability of the humerus.

	Rhamphorhynchoidea (n=13)								Pterodactyloidea (n=11)							
	H	**R/U**	**MC**	**F**	**T**	**MT**	***clr* var**	**% var**	**H**	**R/U**	**MC**	**F**	**T**	**MT**	***clr* var**	**% var**
H		.022	.108	.020	.029	.045	.019	**10.5**		.007	.027	.029	.033	.041	.012	**10.7**
R/U	-.383		.104	.060	.065	.064	.026	**14.7**	-.300		.037	.035	.026	.035	.012	**10.7**
MC	-1.954	-1.571		.172	.175	.041	.050	**28.0**	-1.849	-1.549		.041	.049	.097	.021	**19.4**
F	.168	.551	2.122		.011	.076	.028	**15.8**	.010	.310	1.859		.018	.084	.017	**16.0**
T	-.126	.257	1.828	-.294		.078	.030	**16.7**	-.408	-.108	1.441	-.418		.089	.018	**16.6**
MT	.722	1.104	2.676	.553	.847		.025	**14.3**	.802	1.102	2.650	.792	1.210		.029	**26.6**
	Total variance = .1783								**Total variance = .1080**							

Table 3.15 Variation array matrices for Dyke et al. 2006 Pterosauria data set. The data set was divided accordingly to two-sub orders: Rhamphorhynchoidea and Pterodactyloidea. Abbreviations: H - humerus; R/U – radius/ulna; MC – metacarpal IV; F – femur; T – tibia; MT – metatarsal III.

One could systematize the main variability differences between the two groups of pterosaurs as follows:

- metacarpal and tibia are the elements which contribute at a major scale to the total variance of Rhamphorhynchoidea, while the major sources of variability among Pterodactyloidea are the metatarsal and metacarpal;

- the humerus, femur and tibia reveal similar relative variance in both pterosaur groups;

- Pterodactyloidea is more dissimilar among individuals in hind limb proportions than Rhamphorhynchoidea which is more dissimilar in the fore limb;

- pterodactyloids are more dissimilar among individuals on metatarsal III and more conservative than rhamphorhynchoids in metacarpal IV and radius/ulna proportions.

- in pterosaurs one observes an increase of variability from proximal to distal bones in the fore limb of both groups and in Pterodactyloidea there is a similar trend in the hind limb;

- the metatarsal relative variability in Pterodactyloidea individuals is almost the double than the observed in Rhamphorhynchoidea individuals;

- the main differences of variability are observed in the summed variance of the homologous bones of the zeugopodium and autopodium.

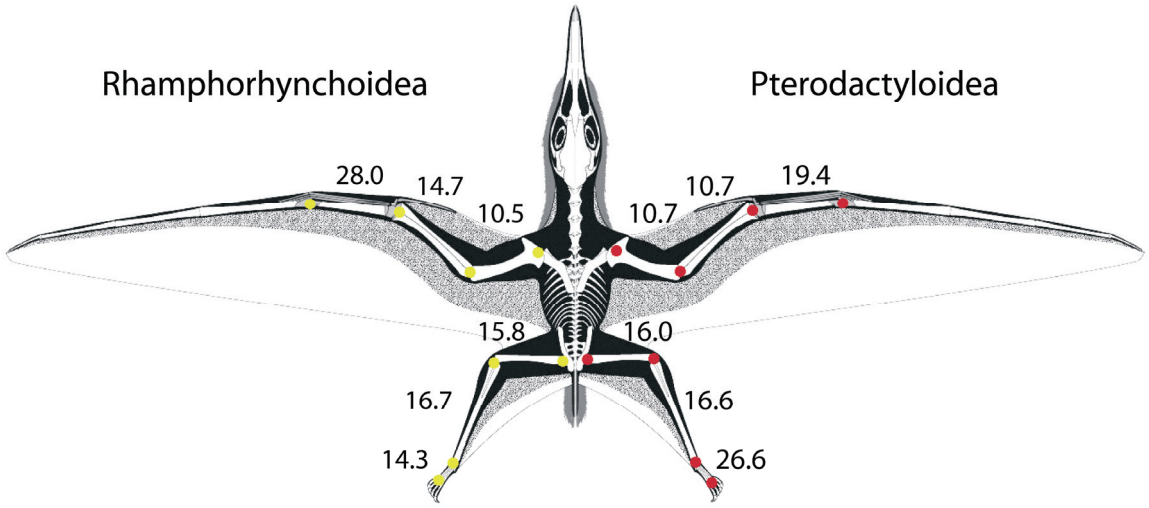

Figure 3.18 Pterodactyloidea and Rhamphorhynchoidea bone proportions variability expressed as percentages of *clr* variance. Generic pterosaur silhouette adapted from John Conway illustration of *Nemicolopterus crypticus* (unpublished).

One has already described the variation of limb bones proportions of the pterosauria combined sample – figure 2.10 b. This biplot, among several other relationships, reveal a small distance between the rays of femur and tibia, fact also observed in Megachiroptera bats.

As one could detect in individual biplots the approximate constant ratio of femur and tibia is also verified within both groups of pterosaurs – figure 3.19 a and b. The individual biplots show different relationships among the limb parts of the two groups of pterosaurs although revealing common patterns. In both groups the autopodium elements are the most important factor for the total variability although the Rhamphorhynchoidea metatarsal has smaller influence than the same bone in Pterodactyloidea. The pterodactyloids main axis of variability is mostly controlled by

metatarsal and radius/ulna and, sequentially with reduced influence since they are controlling PC2, by the metacarpal, tibia, femur and humerus.

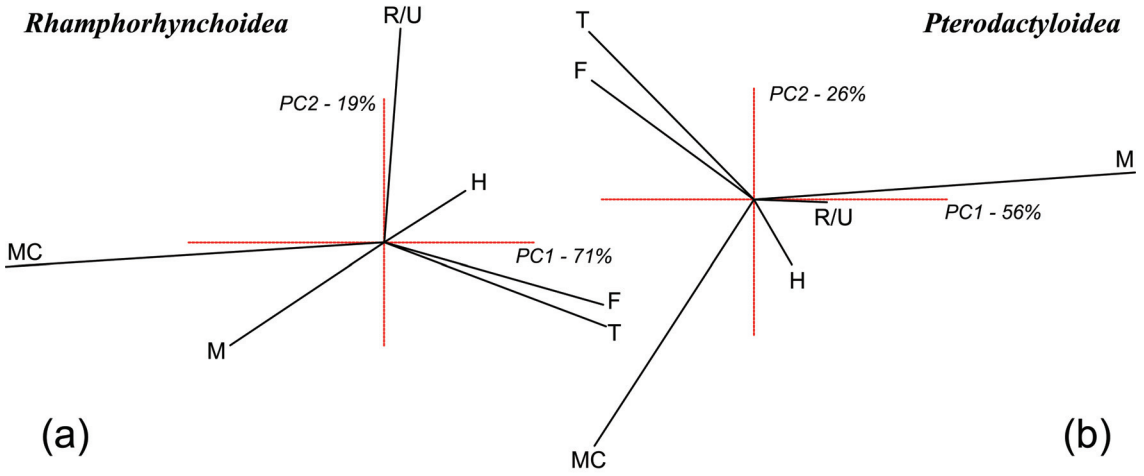

Figure 3.19 a) Biplot of the *clr*-transformed space of the first two principal components (PC1 vs PC2) of Rhamphorhynchoidea sub-sample, six limb parts. First Principal Component (71%), Second Principal Component (19%), Third Principal Component (5%), Fourth Principal Component (4%), Fifth Principal Component (1%). Outliers (not represented in the figure but identified in the biplot analysis) - *Pteranodon sp*. and *Huanhepterus quingyangensis*. b) Biplot of the *clr*-transformed space of the first two principal components (PC1 vs PC2) of Pterodactyloidea sub-sample, six limb parts. First Principal Component (56%), Second Principal Component (26%), Third Principal Component (11%), Fourth Principal Component (6%), Fifth Principal Component (1%). There was any outlier. Abbreviations: H - humerus; R/U – radius/ulna; MC - metacarpal IV; F - femur; T - tíbia; MT - metatarsal III. Dyke et al. 2006 database; see 3.2 for details.

Rhamphorhynchoidea reveals similar variation of parts to Pterodactyloidea although influencing opposite PC's. The main source of influence on PC1 comes from metacarpal and, controlling as well PC2, femur and tibia. One should mention that hind limb autopodium influences both PC1 and PC2 and that its scale on total variability is equivalent to the femur and tibia. PC2 in rhamphorhynchoids is mainly restrained by radius/ulna, oppositely to what is observed on pterodactyloids.

Regarding the explained variability for the first two axes both groups are fairly equivalent (90% for Rhamphorhynchoidea and 82% for Pterodactyloidea) although revealing different percentages for the individual axis.

Resuming, one could suggest that:

- there is an approximately constant ratio between femur and tibia in both groups of pterosaurs (0.75 for Rhamphorhynchoidea and 0.66 for Pterodactyloidea);

- there is a higher influence of radius/ulna in Rhamphorhynchoidea in the total variability than in Pterodactyloidea;

- the autopodium bones are the biggest origin of variability although at different scales for the groups of pterosaurs.

Along this section one could verify that for pterosaur and bat groups the variability of bone parts proportions is distinct. Through different approaches one has identified trends and patterns that could be generally systematized as follows:

- almost half of the total variability in bone proportions originates in the autopodial bones;

- bats fore limb combined proportions are more conservative than the hind limb combined proportions;

- Megachiroptera reveal higher variability than Microchiroptera, mainly in metatarsal III and femur;

- Microchiroptera show higher variability in fore limb proportions than Megachiroptera, due mainly to metacarpal III variability;

- Megachiroptera femur and tibia proportions reveal their ratio is nearly constant. A similar trend was also identified in both pterosaur groups, although with a different ratio.

3.2.5 Balances

Balance	Bone part						Anatomical/Analytical Meaning
	H	R/U	MC	F	T	MT	
B1	**1**	**1**	**1**	**-1**	**-1**	**-1**	fore limb vs. hind limb
B2	**1**	**1**	**-1**	**0**	**0**	**0**	humerus and radius vs. metacarpal
B3	**1**	**-1**	**0**	**0**	**0**	**0**	humerus vs. radius
B4	**0**	**0**	**0**	**1**	**1**	**-1**	femur and tibia vs. metatarsal
B5	**0**	**0**	**0**	**1**	**-1**	**0**	femur vs. tibia

Table 3.16 Sequential binary partition (SBP) used in the balance dendrogram illustrated in figure 3.19. Parts: F – femur; H – humerus; MC – metacarpal III/IV; MT – metatarsal III; R – radius/ulna; T – tibia.

According to table 3.16, the balances will be computed for each sample as follows:

$$B1 = \sqrt{\frac{3 \cdot 3}{3+3}} \ln \frac{(H \cdot R \cdot MC)^{1/3}}{(F \cdot T \cdot MT)^{1/3}},\ B2 = \sqrt{\frac{2 \cdot 1}{2+1}} \ln \frac{(H \cdot R)^{1/2}}{(MC)^{1/1}},\ B3 = \sqrt{\frac{1.1}{1+1}} \ln \frac{(H)^{1/1}}{(R)^{1/1}},$$

$$B4 = \sqrt{\frac{2.1}{2+1}} \ln \frac{(F \cdot T)^{1/2}}{(MT)^{1/1}}, B5 = \sqrt{\frac{1 \cdot 1}{1+1}} \ln \frac{(F)^{1/1}}{(T)^{1/1}}$$

By Balances – complete sample

Observing both the balances dendrogram and the table of the variance decomposition - figure 3.19 and table 3.17 respectively, which sequential binary partition is represented in table 3.16, one distinguishes that the most important balances in terms of variance is B1 (44.1%), followed by B4 (ratio between femur and tibia *vs* metacarpal) with 27.4% of the total variance. B2 (ratio between humerus and radius/ulna *vs* metatarsal) contributes with 15.5% and the least important balances are the homologous B5 and B3, responsible for 7.7% and 5.2%, respectively, of the total variability.

Notice that balance B3 corresponds to the proportional brachial index - humerus vs. radius - is the least variable balance. For some authors this index is informative on the power flight requirements - remind present section introduction - and therefore this fact could be the justification for the least variability since it represents a very strong selective pressure factor.

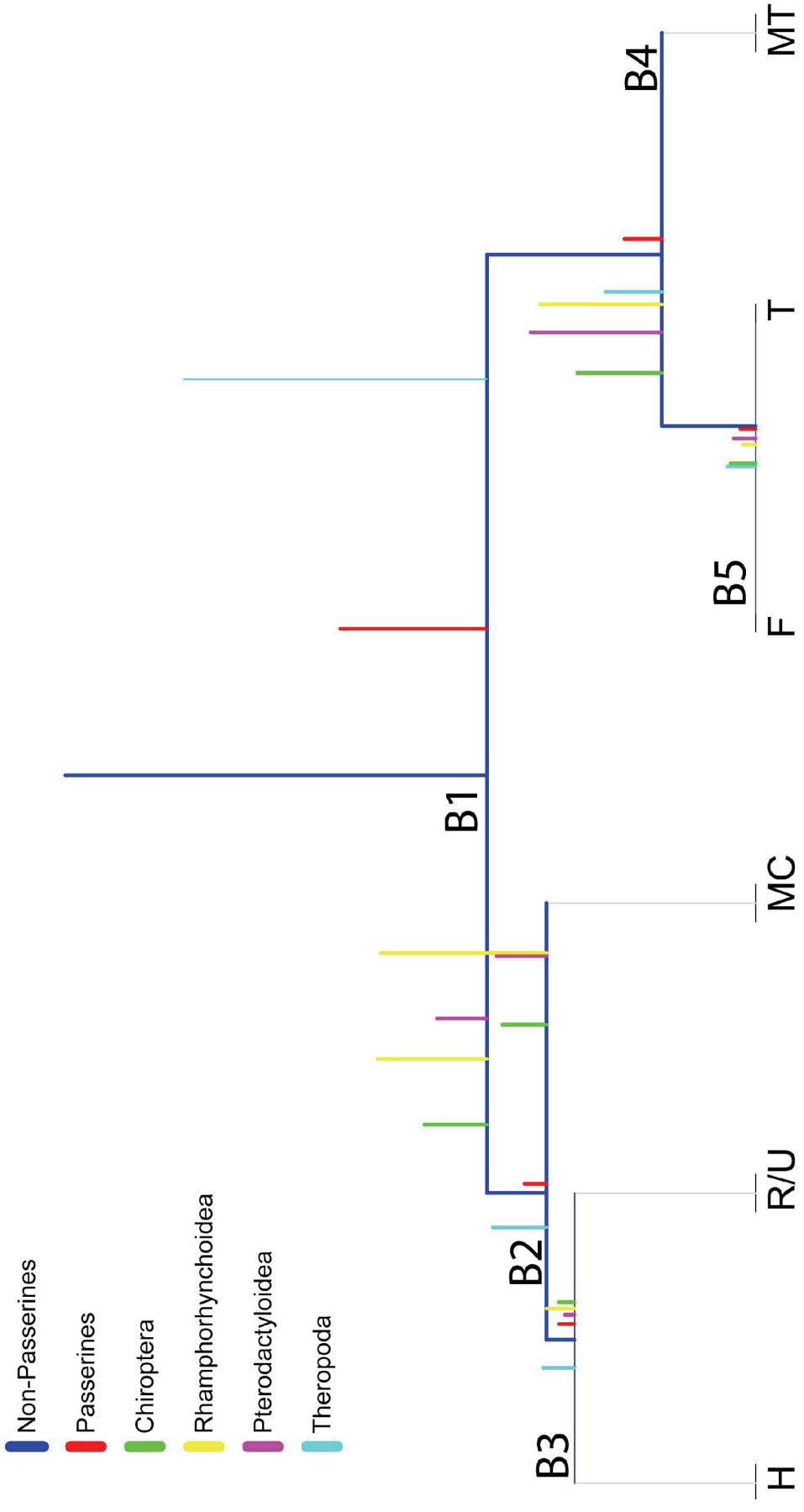

Figure 3.19 Balances dendrogram of flying vertebrates groups: Aves non-Passerines; Aves Passerines; Megachiroptera; Microchiroptera; Rhamphorhynchoidea; Pterodactyloidea; Theropoda. Sequential binary partition indicated in Table 3.18. Abbreviations: F – femur; H – humerus; MC – metacarpal III/IV; MT – metatarsal III; R/U – radius/ulna; T – tibia.

One can, in short and for the complete sample, state that the most influencing balances on the total variability are the ratios of fore limb to the hind limb, B1, followed by the ratio of the hind limb two most proximal bones to the autopodium, B5. The least important factor is the ratio of the fore limb stylopodium to the zeugopodium, B3.

By balances within groups

Among groups each balance has a different impact for the total group variability and one verifies that the balance of the fore limb *vs* hind limb is the most important variability factor in both Aves groups as well as in Theropoda - figures 3.20 and 3.21. Balance B1 constitutes the second most important balance in both groups of Chiroptera and Pterodactyloidea. Note that the balance between limbs (B1) is merely the third most important in Rhamphorhynchoidea, preceded by the homologous balances B2 and B4. Thus, the variability between fore and hind limb proportions in bats and pterosaurs is not as significant as the relative variability observed for the ratios of stylopodium and zeugopodium against the metapodium, that is, the major contribution for the total variability among bats and pterosaur individuals comes mainly from the balance between the hind limb parts and the balance between the two most proximal parts of the fore limb – humerus and radius/ulna.

If one wants to describe the relative importance to the total variability among homologous Balances, or in other words, Balances that compare homologous bones of fore and hind limb, one could state that B4 reveals always higher variability than B2 in all groups except in Rhamphorhynchoidea in which B2 surpasses both B4 and B1. This fact should be interpreted as due to the higher variability of metacarpal. This bone is promoting the variability observed in B2 in Rhamphorhynchoidea. Recall table 3.15 on *clr* variance of the individual bones which revealed that metacarpal variance within Rhamphorhynchoidea individuals is almost the double of the variance in Pterodactyloidea individuals.

Concerning the B3 and B5 one detects that the balances between stylopodium and zeugopodium of both limbs present opposite relative importance in the two groups of pterosaurs and the two groups of bats. Rhamphorhynchoidea individuals show higher relative variability in B3 while Pterodactyloidea present higher variability in the equivalent ratio of the hind limb. This alternation among the ratios of stylopodium and zeugopodium balances could be verified as well in bats since Megachiroptera disclose bigger variability among the B3 - brachial index - while Microchiroptera have that trend in B5.

One could also verify that in both groups the relative interval between B3 and B5 is equivalent. In birds and theropods the deviations involving B3 and B5 is rather distinct from bats and pterosaurs. B3 contribution to the total variability is considerable higher in Non-Passerines than in Passerines and Theropods which present similar percentages of ratio variability. Therefore the variability of the brachial index is considerable superior in Non-Passerines than in Passerines.

The hind limb balance B5 show equivalent and higher relative variability in theropods and Non-Passerines than in Passerines.

By groups

Comparing the relative variability of each group one detects that the most variant group is non-Passerines birds followed, with minor variabilities, by Theropoda, Rhamphorhynchoidea, Pterodactyloidea, Passerines, Microchiroptera and Megachiroptera.

BALANCE	non-Passerines n=601		Passerines n=97		Megachi. n=33		Microchi. n=184		Rhamphorhy. n=13		Pterodactyl. n=11		Theropoda n=14			
		%		%		%		%		%		%		%	var total (by balance)	var % (by balance)
var B1 (Fore vs Hind limb)	.158	**54.3**	.056	**64.4**	.011	**19.3**	.022	**26.8**	.042	**25.5**	.019	**19.4**	.113	**64.6**	.421	**44.1**
var B2 (H and R/U vs MC)	.021	**7.2**	.007	**8.0**	.002	**3.5**	.018	**22.0**	.062	**37.6**	.018	**18.4**	.020	**11.4**	.148	**15.5**
var B3 (H vs R/U)	.011	**3.8**	.005	**5.7**	.006	**10.5**	.004	**4.9**	.010	**6.1**	.003	**3.1**	.011	**6.3**	.05	**5.2**
var B4 (F and T vs MT)	.066	**22.7**	.014	**16.1**	.034	**59.6**	.031	**37.8**	.046	**27.9**	.050	**51.0**	.021	**12.0**	.262	**27.4**
var B5 (F vs T)	.035	**12.0**	.005	**5.7**	.004	**7.0**	.007	**8.5**	.005	**3.0**	.008	**8.2**	.010	**5.7**	.074	**7.7**
var TOTAL (by groups)	.291		.087		.057		.082		.165		.098		.175			
var % (by groups)	**30.5**		**9.1**		**6.0**		**8.6**		**17.3**		**10.3**		**18.3**			

Table 3.17 Variance decomposition for each group and respective balances. Abbreviations: Megachi. – Megachiroptera; Microchi. – Microchiroptera; Rhamphorhy. – Rhamphorhynchoidea; Pterodactylo. – Pterodactyloidea. F – femur; H – humerus; MC – metacarpal III/IV; MT – metatarsal III; R/U – radius/ulna; T – tibia.

In birds the Balance between fore and hind limb represents more than half of the total variability, ranging from 54.3% in non-Passerines to 64.4% in Passerines. The remaining balances follow the hierarchical tendencies of the complete sample except for the ratio between femur and tibia in non-Passerines which is the third most important and exhibiting more than the double percentage of variance of equivalent balance in Passerines.

In the archosaurian groups Aves and Theropoda, B1 is the most important balance regarding the variability among individuals while in bats is the second most important balance and in Rhamphorhynchoidea pterosaurs B1 decreases its relative value to the third most important source of variability.

The variability among pterosaurs and bats is originated mainly by balances where the autopodium bones are involved, that is, balances B2 and B4. If one could suspect this tendency *a priori*, due to higher contribution of both metacarpal and metatarsal to the total limbs length, one should also be expecting that limb ratios would

have a higher variability contribution to the total variability like it could be observable in birds and theropods.

Non-Passerines is the most variant sampled group while bat groups are the two least variant taxa. One could presume that its high limb proportions variability is due mainly to the balance between limbs revealing this way that this group is functionally very dissimilar in fore limb vs. hind limb. Non-Passerines individuals reveal diverse locomotor abilities which allow them to explore different ecological niches and, therefore, this could be the variability factor.

Bats chief locomotor module is the fore limb through active flight constituting this function its main and almost exclusive type of locomotion with some exceptions like the common vampire bat (*Desmodus rotundus*) and the New Zealand short-tailed bat (*Mystacina tuberculata*). These bats have evolved the ability to move well on the ground although in a distinct way of birds (Riskin et al. 2006). Variability within bats limbs should not be as high as in birds since bats hind limb does not contribute as actively to the locomotor function(s) as birds hind limbs, although there is some influence of the bats hind limb in the flight stability.

Diverse groups of birds reveal ecological adaptations that result mainly from selective pressure on the hind limb morphology – e.g. species whose habitat affiliation is mainly the ground, tree or swimmer as identified by Zeffer et al. 2003. As previously identified the majority of hind limb proportions outliers species are classified as belonging to habitats that need intensive use of the hind limbs - table 3.12.

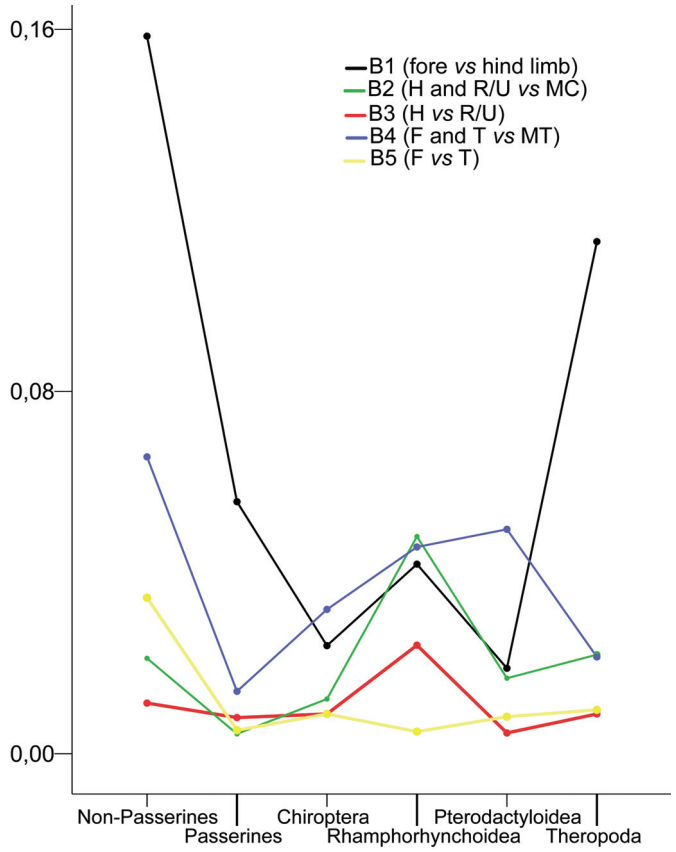

Figure 3.20 Variance for each balance and the complete sample.

The main source of variability among bats is detected in balance B4 – ratio of femur and tibia vs. metatarsal – revealing this way that stylopodium and zeugopodium of hind limb are conservative in proportions despite the above referred *clr* variability of the femur in Megachiroptera. Recalling table 3.14, Megachiroptera is the bat group that sums the biggest percentage of variability in the hind limb and consequently has the least variation among groups in the fore limb. Microchiroptera present a hind limb total variability comparable to non-Passerines. Comparing the balance between humerus vs. radius/ulna among bats one observes that Megachiroptera reveal higher variability in this logratio than Microchiroptera.

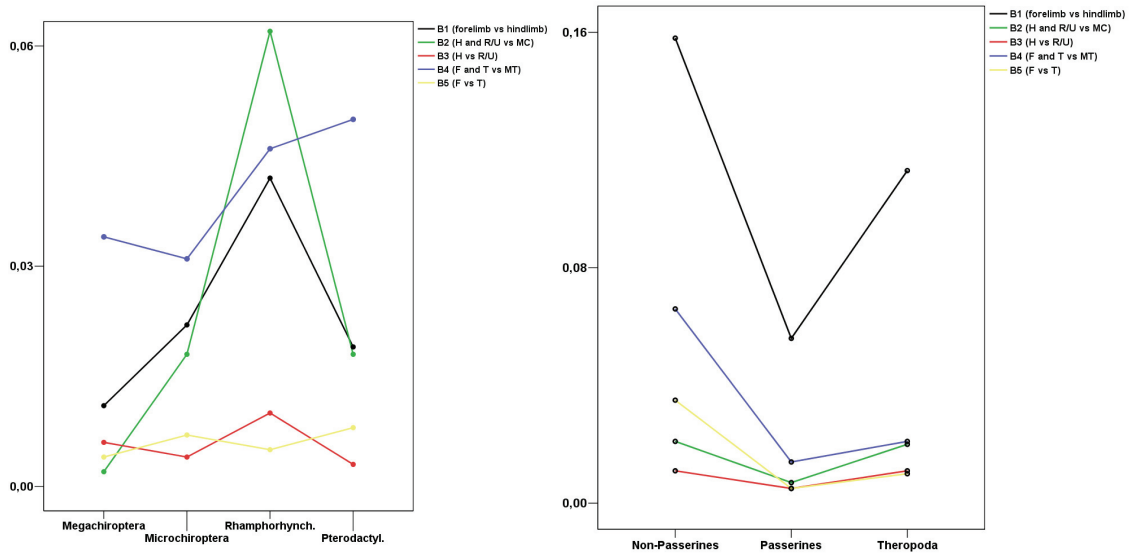

Figure 3.21 a) Variance for each balance of Chiroptera and Pterosauria groups. **b)** Variance for each balance of Aves groups and Theropoda.

Pterosaurs main source of variability arises from three balances – B1, B2 and B4. More than two thirds of the total variability among Rhamphorhynchoidea individuals is originated by B2, which is the logratio between humerus and radius/ulna and metacarpal, followed by B4, between the homologous parts in the hind limb. Thus, more than half of the total variability in rhamphorhynchoids arises when the autopodium bones are integrated in the computation. More than half of Pterodactyloidea variability comes from B4 and could be attributed to metatarsal proportion since B5 – femur *vs* tibia – variability is very low.

Therefore, in both pterosaur groups the major contributions to the total variability among individuals comes from the comparison of proportions between the three bones of each limb, and at a small scale from the logratio between the two limbs.

Size effect

As stated in chapter 2 introduction, one of these work main objectives is to evaluate the variation of bone parts proportions among several groups of organisms.

In order to test the influence of size on distinct balances one have performed several regression analyses of those *ilr* variable (B3, corresponding to the brachial index) on the size of the total fore limb (humerus, radius/ulna and metacarpal III/IV lengths) or the hind limb (femur, tibia and metatarsal III lengths). The total length of each limb was previously log-transformed.

y	x (size)	Group in which size is significant	r ; p	Equation
B3 (H/R)	Fore limb	Megachiroptera	r = 0.646 ; p < 0.01	y = -0.881+0.243*x
	Hind limb	non-Passerines	r = 0,123 ; p < 0.01	y = -0,118 + 0,051*x
		Passerines	r = 0,225 ; p < 0.05	y = -0,315 + 0,131*x
		Megachiroptera	r = 0,650 ; p < 0.01	y = -0,682 + 0,217*x
		Microchiroptera	r = -0,198 ; p < 0.01	y = -0,203 - 0,107*x
		Rhamphorhynchoidea	r = 0,559 ; p < 0.05	y = -0,853 + 0,291*x

Table 3.17 Equations for each group between *ilr*–fore limb length (log transformed) and *ilr*–hind limb length (log transformed); *r* = Pearson's correlation coefficient. Only coefficients that are significant at $p < 0.01$ and $p < 0.05$ are indicated. Abbreviations: B3 - balance B3; H - humerus; R - radius.

Balance B3, which is directly related to brachial index since is the ratio of the proportions of humerus and radius, one has performed a regression analysis of B3 variable on the log transformed fore limb total length.

It should be mentioned that the brachial index that is this analysis was assumed by balance B3 is positively and significantly correlated with the fore limb size only in the bat group Megachiroptera. This fact reveals that Megachiroptera with bigger fore limbs show higher brachial indices with consequent higher power requirements for flight. Megachiroptera bats is, as well, the group showing most variation in balance B3 revealing this way that, among this group, there is distinct flight performances. It is important to mention that Megachiroptera is the only group in which there is a significant correlation between fore limb size and balance B3. Megachiroptera also reveals positive and significant correlation between hind limb size and *ilr* coefficients from balance B3. Oppositely to fore limb, the size of the hind limb is significantly correlated with balance B3 in several groups, namely positively correlated in both Aves

groups (low correlation) and in Rhamphorhynchoidea pterosaurs, and being negatively correlated (low correlation) in Microchiroptera bats.

3.2.6 Final remarks

In the previous sections of this work distinct methods were applied in order to evaluate the proportions variation among pterosaurs, birds and bats. The results have been systematized above. The present section will serve as a more detailed discussion of the results, and also as a broad comparison of the results obtained by the works previously reanalyzed.

Dyke et al. (2006) does not present any quantifiable information regarding pterosaurs, bats or birds morphospace occupation. The present work presents measures (A.D.) of both limbs morphospace occupation, as well as patterns of variability within limb elements of the analyzed taxa.

The existence of a trend in variability among the pterosaur sample has been identified: namely, the variability steadily increases distally in both limbs proportions. This general trend presents one exception: in Rhamphorhynchoidea individuals, the metatarsal III reveals lower variability than the proximal hind limb bones femur and tibia. In Rhamphorhynchoidea, about half of the variability of the metatarsal III of Pterodactyloidea is observable.

One could only speculate that this difference of variability among pterosaur groups autopodium could be linked with distinct areas of wing membrane attachment. Assuming the paradigm of hind limb attachment of pterosaurs flight membrane, introduced in the beginning of this section, one could state that referred autopodial differential variability among pterosaur groups could be justified by the distinct modes of membrane attachment. Pterodactyloids are conceived as having no hind limb membrane connection and, therefore, their autopodium could vary more than in the

rhamphorhynchoids, considered to have some hind limb influence on the membrane attachment.

Middleton and Gatesy (2000; 2006), analyzing taxa morphospaces similar to the ones in the present work, concluded that Chiroptera are, when compared to Aves and Pterosauria samples, the less disparate group in fore limb proportions. In order to reach this conclusion the authors have used the disparity index which deficits have already been commented - section 2.1.2.

The disparity index herein employed, Aitchison Distance, partially contradicts Middleton and Gatesy (2000; 2006) results, since the fore limb less disparate group using a CDA methodology is Passerines birds (A.D. =0.110), followed by bats (A.D. =0.117) and, at close disparity distance, Pterodactyloids (A.D. =0.123).

Since one is analyzing taxa which main locomotor function is associated with the fore limb, it could be stated that this locomotor module is more stable, concerning its proportions and respective A.D., than the secondary module, the hind limb.

This fact could be justified by the superior selective pressure on the main locomotor function which conduces to a more conservative pattern of proportions and consequent lower variability in morphospace occupation.

The ANOVA performed on the intragroups A.D. confirmed that both groups of pterosaurs reveal different patterns of morphospace occupation.

The MANOVA statistical tests performed on the bone proportions confirmed that:

- there are significant differences on the limb proportions when simultaneously comparing all groups and for each limb;

- when the two groups of birds are compared, there are significant differences in limb parts proportions, both in fore and hind limbs;

- when comparing the two groups of pterosaurs there are no significant differences in fore limb parts proportions, whereas there is significant difference in hind limb parts.

Chapter 4 - Sauropodomorpha phylogenetic context and selected groups

"The urge to classify is a fundamental human instinct; like the predisposition to sin, it accompanies us into the world at birth and stays with us to the end."

A. Tindell Hopwood

Proceedings of the Linnean Society of London, The Development of Pre-Linnaean Taxonomy (p. 230) Volume 170, 1959

"Taxonomy is a science, but its application to classification involves a great deal of human contrivance and ingenuity, in short, of art. In this art there is leeway for personal taste, even foibles, but there are also canons that help to make some classifications better, more meaningful, more useful than others."

George Gaylord Simpson

Principles of Animal Taxonomy, From Taxonomy to Classification (p. 107)

4.1 Sauropodomorpha phylogenetic context

The group of animals named Sauropodomorpha at the beginning of the XX century includes some of the biggest Mesozoic terrestrial vertebrates.

Sauropodomorpha dinosaurs belong to Saurischia (Seeley 1887), which was defined by the first numerical cladistic analysis in a dinosaurian context (Gauthier 1986) as a monophyletic clade.

According to von Huene (1932), Sauropodomorpha comprises two lineages: Sauropoda (Marsh 1878) and Prosauropoda (von Huene 1920). The other saurischian clade is Theropoda (Marsh 1881), phylogenetically revised for the first time by Gauthier (1986).

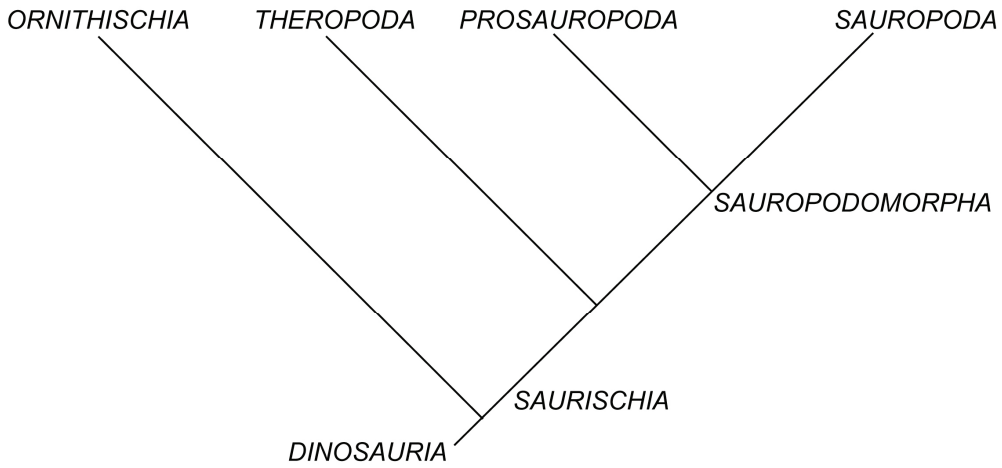

Figure 4.1 Simplifed cladogram of Dinosauria showing the phylogenetic relationships of Saurischia and Sauropodomorpha. Based on Gauthier 1986; Sereno 1998, 1999; Wilson and Sereno 1998.

In the last decade there has been an increasing interest in basal sauropodomorphs, with numerous studies hypothesizing novel higher- and lower-level relationships (Langer et al. 1999; Benton et al. 2000; Galton 2001; Yates 2003a, b, c; Yates & Kitching 2003; Pol 2004; Yates 2004; Bonaparte et al. 2006; Langer and Benton 2006; Sereno 2007a, b; Barrett and Upchurch 2007; Pol and Powell 2007; Upchurch et al. 2007). These phylogenetic proposals were based on the description

and analysis of new material and/or on the revision of previously described sauropodomorph remains.

Among the new sauropodomorph material or new descriptions, one should refer *Antetonitrus ingenipes* (Yates and Kitching 2003), *Ammosaurus major* (Sereno 2007a), *Blikanasaurus cromptoni* (Galton and Van Heerden 1985, 1998), *Lessemsaurus sauropoides* (Pol and Powell 2007), *Melanorosaurus readi* (Bonnan and Yates 2007), *Saturnalia tupiniquim* (Langer et al. 1999; Langer 2003), *Thecodontosaurus caducus* (Yates 2003a), *Thecodontosaurus antiquus* (Benton et al. 2000), *Unaysaurus tolentinoi* (Leal et al. 2004), *Yunnanosaurus huangi* (Barrett et al. 2007). These species contributed, through novel or better material description, to the recent sauropodomorph phylogenetic hypotheses, which will be briefly summarized in this chapter. However, despite the importance of these scientific efforts, most of the basal sauropodomorph phylogenetic relationships (that is, higher- and lower-level) still remain open to debate and inconclusive in the definition of a consensus classification.

Although the main objectives of the present research are not phylogenetically directed, it employs sauropodomorph phylogeny as evolutionary and temporal anchors. In other words, the analysis of the sauropodomorph appendicular skeleton morphology and its morphological evolution here presented must be brought into a phylogenetic context. This context chiefly requires establishing sauropodomorphs major clades interrelationships in order to explore sauropodomorpha appendicular morphological evolution. Despite not proposing new phylogenetic hypothesis, and constrained by the present work's main objectives, which are morphological driven, different phylogenies were reviewed and led to an option for specific ones. The broader options are materialized in figures 4.3 and 4.4, besides being explained along the description of each group used herein.

One fundamental question concerning the phylogeny of Sauropodomorpha regards the monophyly of the clade Prosauropoda. Since the beginning of the 20th

century, prosauropods were, in phylogenetic analysis using either qualitative and/or quantitative methods, considered as being paraphyletic (e.g., Romer 1956; Gauthier 1986; Yates 2003a, 2004, Yates and Kitching 2003; Pol 2004: Pol and Powell 2005; Upchurch et al. 2007), while other authors assumed Prosauropoda as being monophyletic (e.g., Sereno 1989; Galton 1990; Benton et al. 2000; Barrett et al. 2005) – figure 4.2.

In this work the monophyly of Prosauropoda has been implicitly adopted. However, the definition of the monophyly or paraphyly of prosauropods is not the vital purpose of the the present work. Instead, the core question that will be focused on is the phylogenetic proximity of prosauropods to sauropods, as well as the proximity of Sauropodomorpha to its sister taxon Theropoda. Prosauropods and theropods will, therefore, be used as comparison sequential outgroups in order to evaluate patterns of variability in limb proportions of sauropods evolutionary history within a phylogentic framework - see figures 4.1, 4.2, 4.3 and 4.4.

One has herein faced difficulties equivalent to the ones that other researchers that work on non-sauropod sauropodomorphs or integrate them in their analyses had to deal with, namely the non-existence of a general agreement on a consensual classification of this group of dinosaurs.

The goals of the present work, being morphologically driven, merely implicated to discriminate the non-sauropod sauropodomorphs, as described below, at three levels: basal sauropodomorphs, Plateosauria and Sauropodiformes. One has also favored a non-hierarchical internal relationships view of non-sauropod groups (exceptions referred in text and/or clades legend).

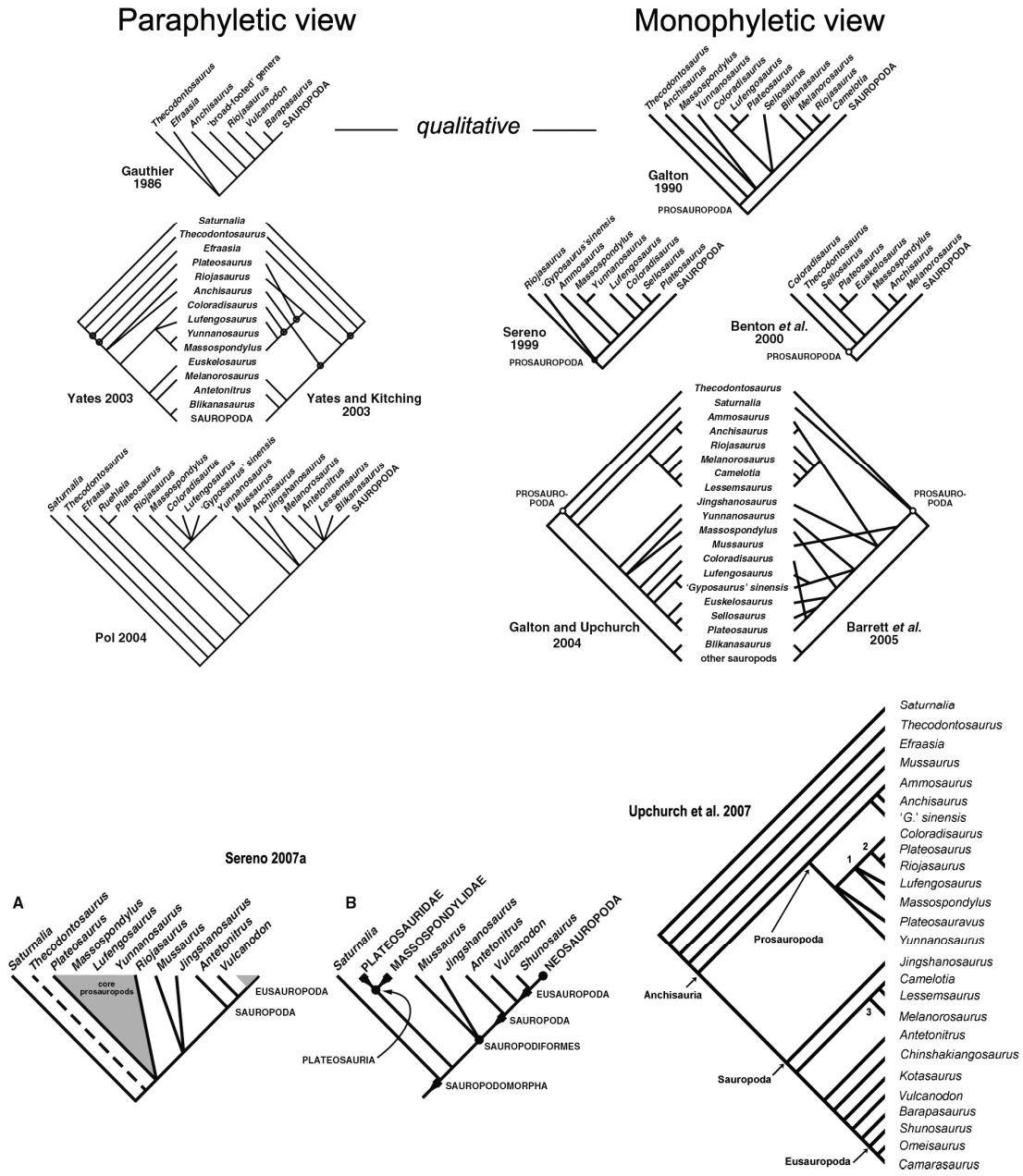

Figure 4.2 Sauropodomorpha phylogenetic hypotheses. Prosauropoda monophyly or paraphyly are indicated, as well as, the qualitative studies - remaing proposals are quantitative. Note that Sereno 2007a proposal for the validity of Prosauropoda depends on the monophyly of 'core prosauropods', indicated in Sereno's summary cladogram (A). Summary cladogram (B) of Sereno 2007a taxonomy implies the availability of Prosauropoda if one excludes Sauropodiformes and unites 'core prosauropods' as a clade. Adapted from Sereno 2007a and Barrett and Upchurch 2007.

Moreover, it was not crucial to assume any non-sauropod internal relationships, a subject which lacks of a general consensus, as one can see on the above mentioned phylogenetic proposals. Only the internal relationships of the basal sauropodomorphs *Saturnalia tupiniquim* and *Thecodontosaurus caducus* was

assumed, since there is a general agreement on both of these species primitive positions within Sauropodomorpha (e.g., Upchurch et al. 2007).

In defining the non-sauropod sauropodomorphs, the phylogenetic proposal of Upchurch et al. (2007) was generally followed, although some nomenclature of Sereno (2005, 2007a), such as Sauropodiformes, has been adopted.

Despite assuming the proposal of Upchurch et al. (2007), it was not fully adopted. For example, *Jingshanosaurus xinwaensis* was thereby positioned as a basal sauropod. Instead, *J. xinwaensis* was herein preferably considered as Sauropodiformes, according to other phylogenetic proposals (Sereno 2007a; Yates 2007) and also corroborated by personal observation of *J. xinwaensis* material (2006) - see details below. Other examples of discrepancy regarding Upchurch et al. (2007) phylogenetic hypotheses are described below.

In short, different and, in most cases, non-compatible phylogenetic hypotheses originated different positionings of the specimens here analyzed. Thus, it was decided to combine different phylogenetic relationships in order to construct a taxonomically congruent cladogram, mainly regarding basal sauropodomorphs and prosauropods, but as well in the Sauropoda clade - figures 4.3 and 4.4.

A secondary factor has contributed to the performed grouping choices: the smallness of the sample size in some groups, which could be an important statistical constraint. Therefore, in this morphometric work and subsequent statistical analysis, it has been chosen to aggregate some of the previously constructed groups into major categories - see below groups B to E in figure 4.5, and compare with figures 4.3 and 4.4.

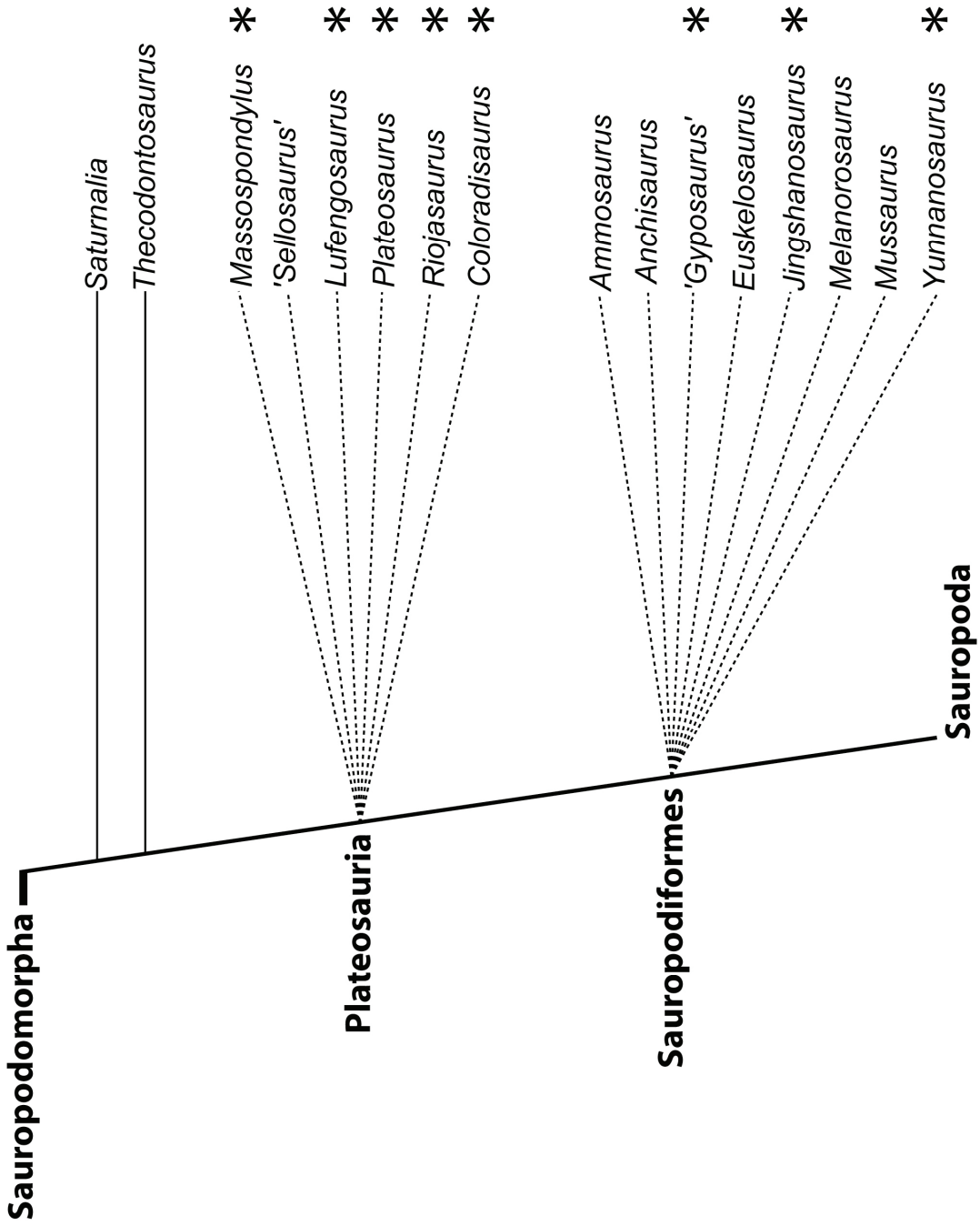

Figure 4.3 Sauropodomorph species and interelationships used herein, based on the following phylogenetic hypothesis: Yates 2003a; Sereno 2007a; Upchurch et al. 2007; Yates 2007. Dashed lines reflect absence of ingroup relationship. Solid lines imply ingroup relationships. * Specimens that have been personally observed.

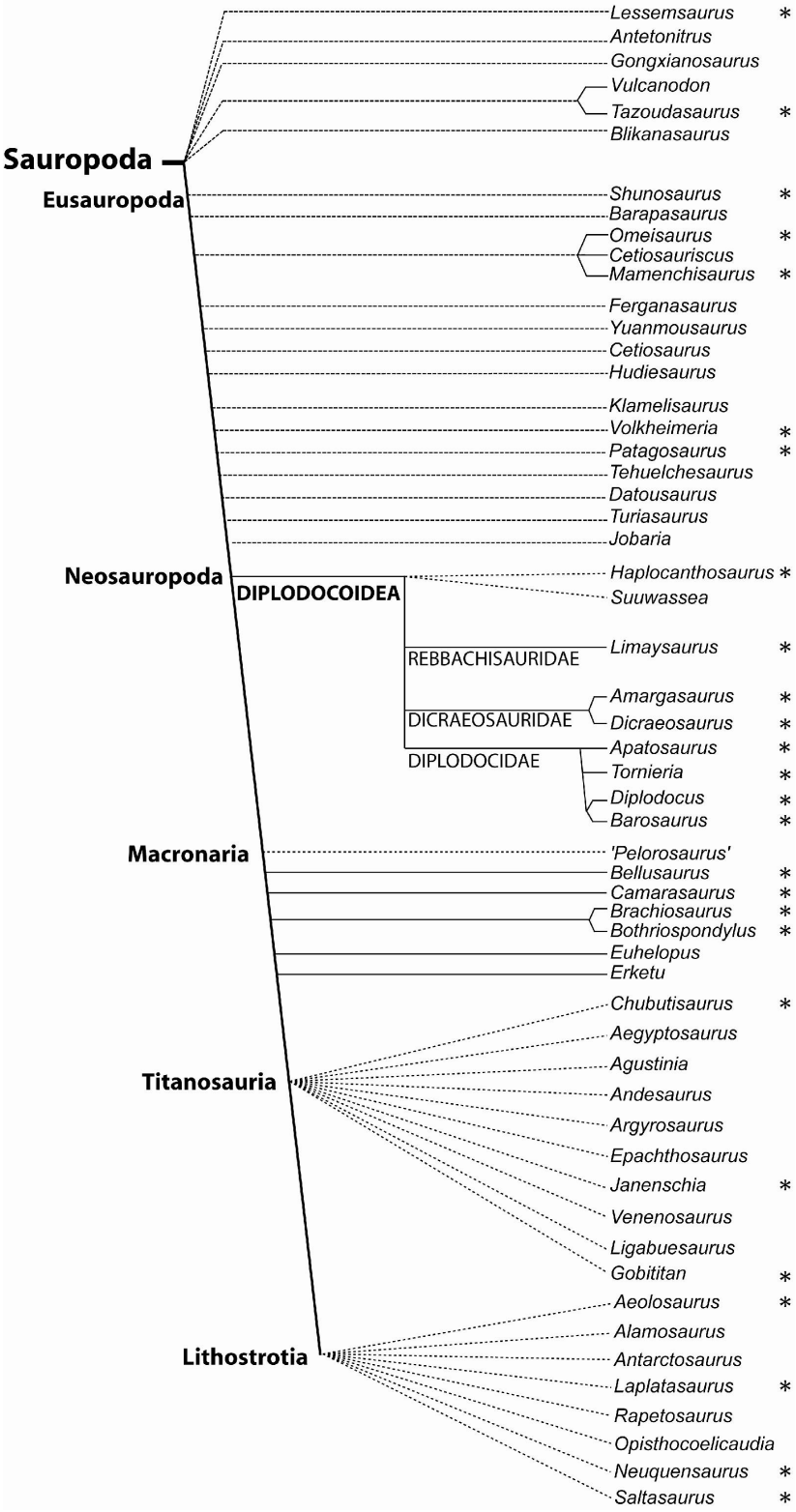

Figure 4.4 Sauropod species and interrelationships used herein, based on the following phylogenetic hypothesis: Upchurch 1998; Wilson and Sereno 1998; Wilson 2002, 2006; Upchurch et al. 2004; Rauhut et al. 2005; Remes 2006; Royo-Torres et al. 2006. Dashed lines reflect absence of ingroup relationship resolution. Solid lines imply ingroup relationships. Taxonomical nomenclature not mentioned in text: Rebbachisauridae Bonaparte 1997, Diplodocoidea Upchurch 1995, Dicraeosauridae Janensch 1929a, Diplodocidae Marsh 1884. * Specimens that have been personally observed.

In the next sections, the Sauropodomorpha groups used in this work will be described and accompanied by a justification of the criteria used.

4.1.1 Definition of the major Sauropodomorph clades used in this study

Genus-level classification of Sauropodomorpha is depicted in figure 4.5, where major clades used in this study are phylogenetically nested. In this part of the work, the definition(s) provided by different authors for each clade were reviewed and summarized.

(1) Node Sauropodomorpha. Distinct cladistic studies – both numerical and non-numerical – presently support the monophyly of Sauropodomorpha (Gauthier 1986; Sereno 1999; Langer 2004). This group was defined as a node-based taxon, including "... the most recent common ancestor of Prosauropoda and Sauropoda and all of its descendants" (Salgado et al. 1997a, p. 6). Sauropodomorpha was defined as a stem-based taxon that includes "*Saltasaurus loricatu*s Bonaparte and Powell 1980 but not *Passer domesticus* (Linnaeus 1758), *Triceratops horridu*s (Marsh 1889)" (Sereno 1999, 2007).

(2) Terminal taxon Plateosauria. Plateosauria is a clade that has been defined as a node-based taxon, containing the most recent common ancestor of Plateosauridae and Massospondylidae and all of that ancestors descendants (Sereno 1998, 1999). The Plateosauria clade is here used as an equivalent, in the bulk of the specimens, to 'core prosauropods', a term used as a "clade that unties basal sauropodomorphs more advanced than 'core prosauropods' but less advanced than taxa that might be regarded as basal sauropods." (Sereno 2005; 2007a, p. 24) and which consists of five genera: *Plateosaurus*, *Massospondylus*, *Lufengosaurus*, *Yunnanosaurus* and *Riojasaurus*.

(3) Terminal taxon Sauropodiformes. Sereno (2005 and 2007a) defined Sauropodiformes as a "clade that unties basal sauropodomorphs more advanced than

'core prosauropods' but less advanced than taxa that might be regarded as basal sauropods." (Sereno 2007a, p. 24) This group was erected due to the necessity of joining the most advanced non-sauropod species not previously included in basal sauropodomorphs.

(4) Node Sauropoda. Sauropoda comprise one of the most successful groups of dinosaurs, both in terms of temporal and geographical distribution, besides being one of the most diverse lineages of this type of animals. These factors, associated with some of its morphological singular characteristics, such as extremely long and slender neck and proportionally undersized skulls, a tremendous body mass in most of the species supported by four columnar limbs, always mesmerized both professional and amateurs.

Since the first description of a sauropod – *Cetiosaurus*, accomplished by Richard Owen, who in 1841 proposed the name Dinosauria - that sauropods contributed to the immense fascination of dinosaurs natural history. The term Sauropoda was originally erected by O.C. Marsh in 1878 and many features listed in the initial diagnosis "are now well-corroborated synapomorphies for the group or for more exclusive sauropod subgroups that were not identified at the time of Marsh's writing" (Wilson 2005a, p. 16).

Sauropoda was defined as a stem-based taxon, which includes "sauropodomorphs more closely related to *Saltasaurus* than to *Plateosaurus.*" (Wilson and Sereno 1998, p. 24) and as a node-based taxon, containing "...the most recent common ancestor of *Vulcanodon karibaensis* and Eusauropoda and all of its descendants" (Salgado et al. 1997a, p. 6).

Studies on both internal and external relationships of the clade Sauropoda received modest attention until ten years ago, when compared with other groups of dinosaurs, for example Theropoda.

The first large cladistic analysis on sauropods was presented by Upchurch (1995), in which a dataset with 125 synapomorphies was presented. This seminal work was preceded by some initial contributions (Yu 1990; Wilson & Sereno, 1994; Calvo and Salgado, 1995). In the following years of Upchurch's contribution, other researchers examined sauropod evolutionary relationships, increasing the knowledge of the internal relationships of this group (Upchurch 1998; Wilson and Sereno 1998; Wilson 2002; Wilson and Upchurch 2003). These reference works served as a guide for others that focused on different aspects of sauropod paleobiology, namely on locomotion, that will be reviewed in the next chapter (e.g. Carrano 1999, 2005; Bonnan 2001, 2003, 2004; Wilhite 2003, 2005; Bonnan and Senter 2007; Bonnan and Yates 2007).

Previous proposed phylogenetic hypotheses, integrating numerous osteological characters, supported the monophyly of Sauropoda, as well as that of its subgroup Eusauropoda (Upchurch 1995, 1998; Wilson 2002, 2005a; Wilson and Sereno 1998).

(5) Terminal taxon non-Eusauropoda. In the phylogenetic relationships of basal sauropodomorphs, there is much controversy regarding the morphological and taxonomical "frontier" among derived sauropodomorphs and "true" sauropods. Even in the former, the general agreement only starts with the Eusauropoda clade. Consequently, the use of a generally employed but formally undefined group, comprising diverse basal sauropods, was favored and named non-Eusauropoda sauropods.

(6) Node Eusauropoda. Eusauropoda was proposed as a clade that includes two monophyletic groups: the Euhelopodidae and the more derived clade Neosauropoda (Upchurch 1995). Recently, Eusauropoda was defined as "the node-based group including *Shunosaurus lii, Saltasaurus loricatus*, their most recent common ancestor, and all descendants." (Wilson 2005a, p. 27)

(7) Terminal taxon non-neosauropod Eusauropoda. The group non-Neosauropoda Eusauropoda was used in order to accommodate eusauropods more derived than basal sauropods, but not included in the clade Neosauropoda. It should be mentioned that “Although relationships within Neosauropoda are well supported, its origin from non-neosauropod taxa is not.” (Wilson 2002, p. 247).

(8) Node Neosauropoda**.** Neosauropoda is the node-based group including *Diplodocus longus, Saltasaurus loricatus* and all descendants of their most recent common ancestor (Wilson and Sereno 1998, fig. 1.4). This definition implies the existence of “…two stem-groups (Diplodocoidea, Macronaria)…” (Wilson 2005a, p. 27).

(9) Terminal taxon Diplodocoidea. The attribution of the name Diplodocoidea is both due to Marsh (1884) and Upchurch (1995), being Upchurch the first to use it explicitly and define Diplodocoidea as “a new superfamily which contains the Diplodocidae, Dicraeosauridae and the new family, Nemegtosauridae” (Upchurch 1995, p. 380). Diplodocoidea is also defined as a stem-based taxon comprising “All neosauropods closer to *Diplodocus* than to *Saltasaurus*” (Wilson and Sereno 1998, p. 55).

(10) Node Macronaria. Some of the most well and long known sauropod species are included in this group. The formal definition of Macronaria by Wilson and Sereno (1998) includes all neosauropods more closely related to *Saltasaurus loricatus* than to *Diplodocus longus* (Wilson and Sereno 1998, p. 49).

(11) Node Titanosauria. Titanosauria was defined as “Titanosauriforms more closely related to *Saltasaurus* than to either *Brachiosaurus* or *Euhelopus*” (Wilson and Sereno 1998, p. 22). Titanosaurs present diverse paleobiological peculiarities and include both the smallest and largest sauropods and were one of the most diverse sauropod clades.

(12) Terminal taxon Lithostrotia. Lithostrotia was erected as a node-based group including *Malawisaurus* and more derived titanosaurs, which share the presence of dermal armour (Upchurch et al. 2004).

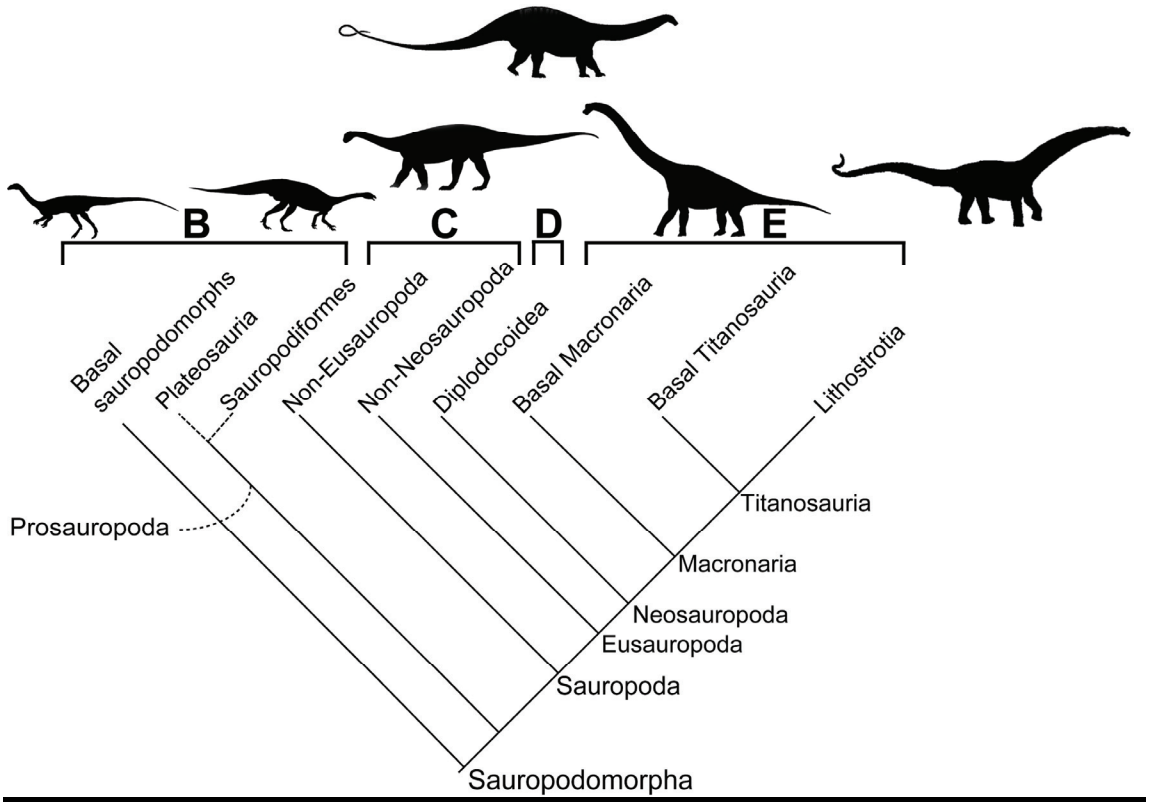

Figure 4.5 Sauropodomorpha generic classification and groups used in this work – nomenclature and ingroup relationships follows the phylogenies described in text and illustrated in figures 5.3 and 5.4. It should be noted that some specimens were not included as specified in the referred phylogenies (description and discussion in text). Groups collapsed, for ease of comparison and statistical validity of the analysis: B - Non-sauropods sauropodomorphs; C - Non-neosauropods sauropods; D - Diplodocoids sauropods; E - Macronarians sauropods. Silhouettes of *Saturnalia tupiniquim*; *Plateosaurus engelhardti*; *Gongxianosaurus shibeiensis; Apatosaurus*; *Brachiosaurus*; *Futalognkosaurus dukei* based in Langer and Benton 2006; Yates 2003b; Wilson 2005a; Wilson and Sereno 1998; Wilson and Sereno 1998; Calvo et al. 2007, respectively. Specimens are not all at the same scale.

4.2 Sauropodomorph groups used

The data analyzed herein combine “traditional” (limb bone lengths) measurements in an evolutionary framework. Detailed morphlogical description of the biological materials (bone elements) used in this work is given in the present chapter, as well as in chapter 5.

The data were collected first-hand from a wide-ranging material of sauropodomorphs of diverse origins, gathering a wide biogeogeographic and chronological spectrum - see Appendix 1. The task of data studying and collecting in natural history museums and other institutional collections all over the world took almost one and a half years, due mainly to logistic and monetary reasons, but also to the type of osteological material involved in this analysis.

The phylogenetic context provided in this study is based on the following categories: A, Dinosauromorpha; B, non-sauropod sauropodomorphs; C, non-neosauropod sauropods; D, diplodocoid sauropods; E, macronarian sauropods - see figures 4.5. and 6.3. Studied species have been gathered according to these categories - see Appendix 1. The measured specimens have been listed and the bibliographic sources from part of the analyzed data have been compiled In the Appendix 1, as well as in chapter 6. The sample comprises 28 genera of sauropodomorphs, some genera (e.g., *Plateosaurus*, *Camarasaurus*, *Apatosaurus*, *and Cetiosaurus*) being overrepresented.

To each category a brief summary of the studied species, with insights on their phylogenetic attributions, was provided.

Category A DINOSAUROMORPHA SERENO, 1991

Specimens included in this group: *Silesaurus opolensis* Dzik 2003, *Lagosuchus talampayensis* Romer 1971, *Marasuchus lilloensis* Sereno 1994, *Lagerpeton chanarensis* Romer 1971, *Guaibasaurus candelariensis* Bonaparte et al., 1999, *Staurikosaurus pricei* Colbert 1970; Galton 1977.

Dinosauromorpha refers to the clade comprising Neornithes and all ornithodirans closer to Neornithes than to Pterosauria" (Sereno 1991, cited by Benton 2004, p. 15)

Category B1 (BASAL) SAUROPODOMORPHA VON HUENE, 1932

Specimens included in this group: *Saturnalia tupiniquim* Langer et al. 1999; *Thecodontosaurus caducus* Yates 2003a.

Saturnalia tupiniquim is the most basal sauropodomorph (Langer et al. 1999; Langer 2002; Sereno 2007a, b; Yates 2003a, b; Yates and Kitching 2003). The appendicular skeleton of *S. tupiniquim* presents some similarities with other basal sauropodomorphs, namely short and robust forelimbs, as well as slender metatarsals. The hind limb of *Saturnalia* is roughly double the length of the fore limb, with similar proportion as in theropods (Huene 1926, Raath 1969, Welles 1984), bipedal ornithischians (Thulborn 1972, Santa Luca 1980) and *Herrerasaurus* (Novas 1994, Sereno 1994). Prosauropods, oppositely, have longer fore limbs (Galton 1976; Cooper 1981; Bonaparte and Pumares 1995), with more than half the hind limb length.

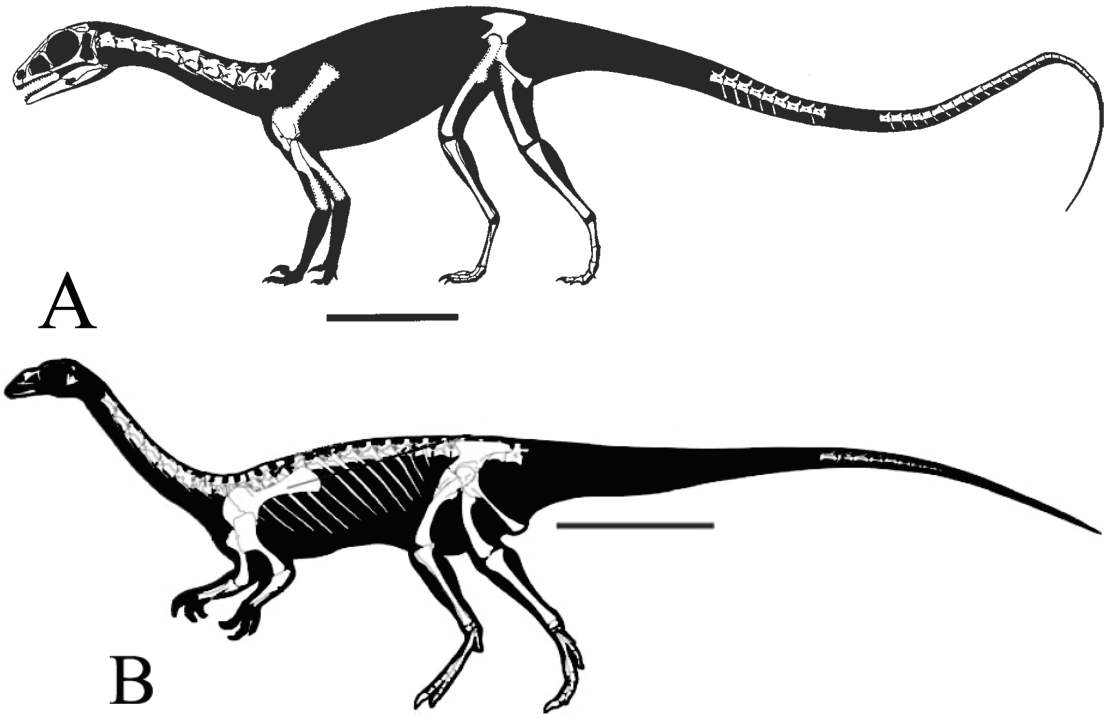

Figure 4.6 Skeletal reconstructions of (A) *Thecodontosaurus caducus* and (B) *Saturnalia tupiniquim*. Adapted from Yates 2003a and Langer and Benton 2006, respectively. Scale bars 0.1 m and 0.25 m, respectively.

Thecodontosaurus caducus is, along with *Saturnalia*, the most basal sauropodomorph (e.g., Barrett et al. 2005; Galton and Upchurch 2004; Pol 2004), although more derived than *Saturnalia*. These two genera form successive sister-taxa to all sauropodomorphs. It should be recalled that all sauropodomorphs more derived than *Thecodontosaurus* "form a well-supported clade." (Yates 2003a, p. 23).

Category B2 (PROSAUROPODA VON HUENE 1920); PLATEOSAURIA TORNIER, 1913

Specimens included in this group: *Coloradisaurus brevis* Bonaparte 1969, 1972 (pers. obs. 2006)*; Lufengosaurus huenei; Lufengosaurus magnus; Massospondylus carinatus* Owen 1854 (pers. obs. 2007)*; Massospondylus sp.; Plateosaurus engelhardi* Meyer 1837 (pers. obs. 2006)*; Plateosaurus robustus* Huene 1932*; Plateosaurus sp.; Plateosaurus trossingensis* Fraas 1913[*] (pers.obs. 2006)*; Riojasaurus incertus* Bonaparte 1978 (pers. obs. 2006)*; 'Sellosaurus gracilis'* Huene 1907-08.

[*] *Plateosaurus trossingensis* is a subjective synonym of *Plateosaurus longiceps* (Galton and Upchurch 2004).

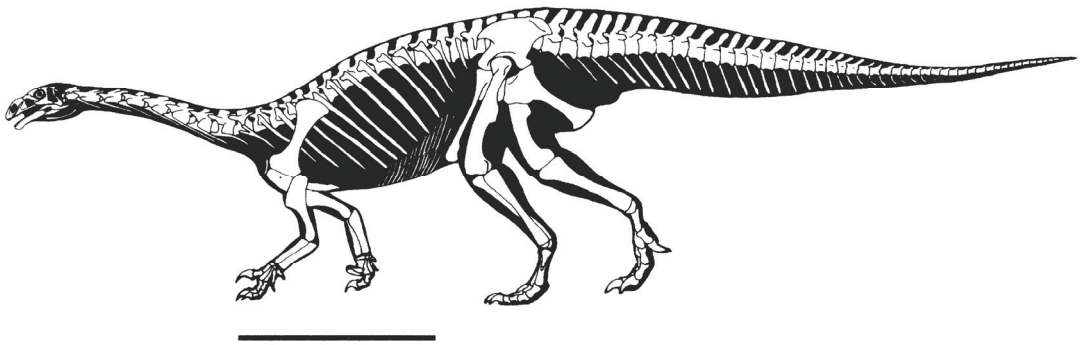

Figure 4.7 *Plateosaurus engelhardti*. Adapted from Yates 2003b. Scale bar represents 1 m.

In this work Upchurch (2007) definition of *Plateosauria* has been followed, which "currently includes Plateosauridae, *Massospondylus* and possibly *Lufengosaurus,* but would exclude *Yunnanosaurus* and *Plateosauravus*." (Upchurch et al. 2007, p. 64). The same classification statement was used herein to include in this group *Lufengosaurus huenei* and *Lufengosaurus magnus* (pers. obs. 2006), as well as *Massospondylus carinatus* and *Massospondylus* sp.

The morphometric data of the genus *Plateosaurus* here analysed includes several species: *Plateosaurus engelhardi* (pers. obs. 2006), *Plateosaurus robustus*, *Plateosaurus sp*. and *Plateosaurus trossingensis* (pers. obs. 2006). A detailed revision of this genus was recently completed (Yates 2003b) and the relationships among species established.

Since *'Sellosaurus gracilis*' is "indistinguishable from a small specimen of *Plateosaurus*" (Yates 2003a, p. 21), and therefore could be attributed to that genus, this species is included herein in the Plateosauria group.

Coloradisaurus brevis (pers. obs. 2007) and *Riojasaurus incertus* (pers. obs. 2007) are Triassic taxa from the Villa Unión-Ischigualasto Basin (northwestern Argentina), belonging to Plateosauria (Upchurch et al. 2007) or non-eusauropod sauropodomorphs (Pol and Powell 2007). Adopting the first proposal, these taxa were included in Plateosauria, thus establishing a closer relationship between the genus

Plateosaurus and *R. incertus* and both sister-groups to *C. brevis*, this one being less derived than the latter. This hierarchical ingroup statement was not assumed herein.

Category B3 SAUROPODIFORMES SERENO 2005, 2007A

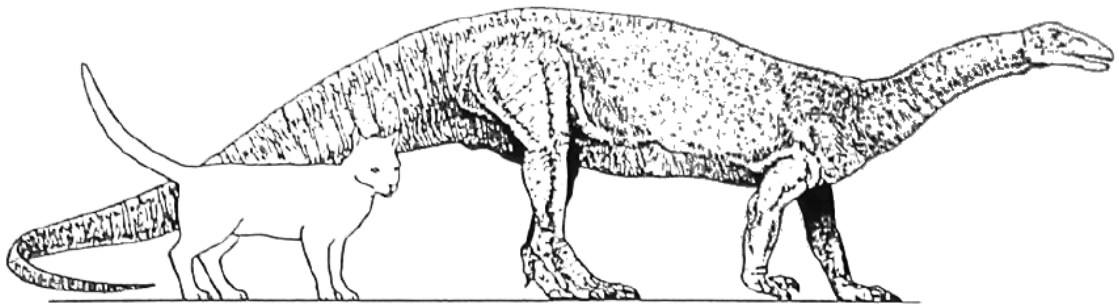

Figure 4.8 *Anchisaurus polyzelus* reconstruction. Adapted from Gauffre 1996.

Specimens included in this group: *Ammosaurus major* Marsh 1889*; Anchisaurus polyzelus* Yates 2004*; 'Gyposaurus' sinensis* Young 1941 (pers. obs. 2006)*; Euskelosaurus browni* Huxley 1866*; Jingshanosaurus xinwaensis* Zhang and Yang 1994 (pers.obs. 2006*); Melanorosaurus readi* Van Heerden 1979; *Mussaurus patagonicus* Bonaparte and Vince 1979*; Yunnanosaurus huangi* Young 1942 (pers.obs.2006).

Despite partly following the internal relationships, as well as the nomenclature of Sauropodiformes, it has been decided to include in this group some specimens that have not been previously included by the proposer of this taxon (Sereno 2005, 2007a).

'Euskelosaurus browni' is now considered as *Plateosauravus* according to Upchurch et al. (2007), which assumed previous studies (Yates 2003c) and related *'E. browni'* to sauropods, but as an outgroup of them (Yates 2003a). Following Yates (2003a) proposal, the more derived state of *E. browni* was adopted, including it in Sauropodiformes.

The embryonic material of *Mussaurus patagonicus* from the Late Triassic of Argentina allowed its inclusion in Sauropodiformes (Sereno 2007a). Others considered *M. patagonicus* as basal sauropodomorph (Barrett et al. 2005; Barrett and Upchurch 2007) and therefore, as justified above, "equivalent" to the Sauropodiformes definition used in the present work. Although *M. patagonicus* presents derived cranial features

(Casamiquela 1980; Pol 2004; Pol and Powell 2005), its limbs are very similar to other basal sauropodomorphs.

The appendicular similarities observed in *Jingshanosaurus xinwaensis* (pers. obs. 2007) with both basal sauropodomorphs and prosauropods could also be used to favour its inclusion in this work in the group Sauropodiformes (Sereno 2007a; Yates 2007) rather than in basal Sauropoda (Yates 2003, 2004; Yates and Kitching 2003; Galton and Upchurch 2004; Upchurch et al. 2007). The *manus* material observed is very similar to those of other prosauropods and basal sauropodomorphs (pers. obs. 2006). Cumulatively, the short fore limb and long trunk also compelled the present work to prefer a non-sauropod origin for *J. xinwaensis* over its inclusion in Sauropoda.

The "near-sauropod" sauropodomorph *Melanorosaurus readi* was recently considered as a basal (non-Eusauropoda) sauropod (e.g., Yates and Kitching 2003; Yates 2004; Upchurch et al. 2007). Nevertheless, other internal relationships of sauropodomorphs regard *M. readi* as an outgroup to sauropods and state that " '*Euskelosaurus*', *Melanorosaurus* and *Blikanasaurus* form serially closer outgroups to the Sauropoda (*Vulcanodon* + Eusauropoda)." (Yates 2003a, p. 23).

Moreover, another analysis, following the "traditional" view of this species, excludes *M. readi* from the heterodefinitional synonym of Sauropoda – Massopoda tax. nov. Yates 2007- which is defined "as the most inclusive clade that includes *Saltasaurus loricatus* but not *Melanorosaurus readi*" (Yates 2007, p. 104).

The cited phylogeneteic hypotheses compelled our decision to include *M. readi* in Sauropodiformes, although the term "Massopoda" has not been adopted.

Also included in 'core prosauropods" (Sereno 2007a), the Chinese species *Yunnanosaurus huangi* (pers. obs. 2007) was incorporated in the previous group Plateosauria. The reason for this option is based on one of the most recent phylogenetic hypotheses proposed for basal sauropodomorphs, which stated "*Massospondylus* appears to be more closely related to 'plateosaurids' than is

Yunnanosaurus." (Upchurch et al. 2007, p. 65). Despite moving out *Yunnanosaurus* from Sereno's 'core prosauropods' and putting it in a clade defined by the former – *Sauropodiformes* – this option, apparently paradoxical, seemed reasonable to us, since, as described above, this work uses phylogenies as a tool and does not have the purpose of reworking the phylogenetic hypotheses previously proposed.

The small and facultatively bipedal sauropodomorph *Anchisaurus polyzelus* from North-America is implicated in abundant taxonomical debate. Traditionally regarded as a prosauropod (Sereno 1999), a recent classification integrates it as a sub-set of Prosauropoda with *Ammosaurus* and the Melanorosauridae (Galton and Upchurch 2004) or as being part of a clade that contains Plateosauria and a clade comprising *Anchisaurus, Alamosaurus* and *'Gyposaurus'* (Upchurch et al. 2007).

The above cited classifications imply that *A. polyzelus*, *Ammosaurus major* and *'Gyposaurus' sinensis* (pers. obs. 2007) should be regarded as less derived than species that are part of the group Sauropodiformes as established in this work (e.g., *Coloradisaurus brevis* or *Plateosaurus engelhardi*). However, other phylogenetic analyses support that *A. polyzelus* is more closely related to Sauropoda (Yates 2004, 2007) placing it and *A. major* in a position more derived than the genus *Plateosaurus* or *Lufengosaurus*.[†]

Category C1 NON-EUSAUROPOD SAUROPODA

Specimens included in this group: *Antetonitrus ingenipes* Yates and Kitching 2003*; Blikanasaurus cromptoni* Galton and Van Heerden 1985*; Gongxianosaurus shibeiensis* He et al. 1998; *Lessemsaurus sauropoides* Bonaparte 1999b (pers.obs.2006); *Tazoudasaurus naimi* Allain et al. 2004 (pers.obs. 2006)*; Vulcanodon karibaensis* Raath 1972.

[†] Note that: a) *A. polyzelus* and *A. major* are considered as synonyms (Sereno 1999, 2007; Yates 2003) being *A. major* a junior synonym of the *A. polyzelus*; b) *Gyposaurus sinensis* are regarded as a juvenile form of *Lufengosaurus* (Yates 2003a). In this work the above cited phylogenetical statements are not adopted and both synonyms as well as juvenile individuals are considered as being distinct species although some ontogenetic considerations are made in chapter 6.

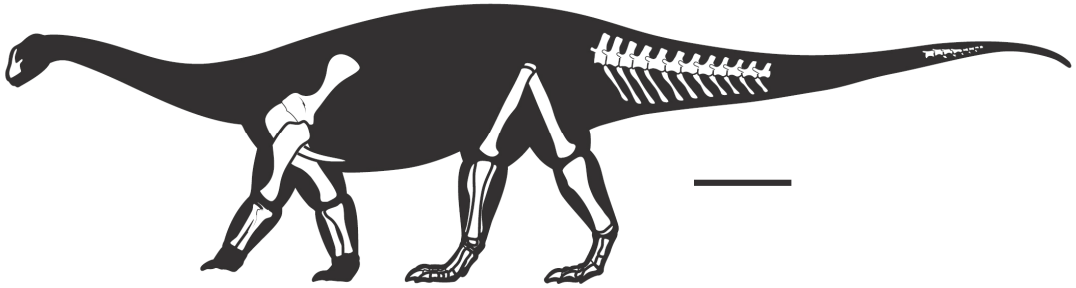

Figure 4.9 *Gongxianosaurus shibeiensis* silhouette skeletal reconstruction and known parts of skeleton. Note the relative proportions of fore- and hindlimb. Adapted from Wilson 2005a. Scale bar represents 1 m.

In the assembling of this group the definition of Eusauropoda was present in order to accommodate diverse sauropods less derived than that clade – see definition of the next group.

Lessemsaurus sauropoides (pers. obs. 2006) is herein considered as a basal sauropod, following the sauropod internal relationships for this species (Yates 2007; Upchurch et al. 2007), which relocate the previous inclusion in Melanorosauridae (Bonaparte 1999b) or in Sauropodomorpha (Pol and Powell 2007). Despite *L. sauropoides* being considered, by the referred analysis, closely related to *Melanorosaurus readi*, it was included in the sauropodiformes group due mainly to the phylogenetic arguments of Yates 2007 (p. 104).

The large-bodied *Blikanasaurus cromptoni* was traditionally included in the Prosauropoda clade (Galton and Van Heerden 1985; 1998). Even with the recent interest in derived sauropodomorphs and basal sauropods, this species was still considered a near-sauropod sauropodomorph (Pol 2004; Yates 2003a). New analyses provided new in-group relationships of basal sauropodomorphs and place *B. cromptoni* in a basal position in the Sauropoda clade (Galton and Upchurch 2003; Yates 2004; Upchurch et al. 2007). Regardless of the fact that only the hind limb and *pes* are known from this animal and the consequent instability of this taxon in any phylogenetical analysis, its inclusion in the non-Eusauropoda group has been favored.

Antetonitrus ingenipes was considered more derived than other basal sauropodomorphs in the phylogenetic analysis of the original description work, which placed it “at the base of Sauropoda, in a polytomy with *Isanosaurus*, *Blikanosaurus* and a clade containing *Kotasaurus*, *Vulcanodon* and Eusaropoda” (Yates and Kitching 2003, p. 1755).

The large morphological similarities observed between *Lessemsaurus* and *Antetonitrus* were noted by other authors, who stated the probable relationship between the fauna from the Elliot Formation in South Africa and the Los Colorados Formation in Argentina (Pol and Powell 2007). *A. ingenipes* represents a transitional form from the gracile *bauplan* of prosauropods to the more robust and graviportal general form of sauropods, confirming its basal position in the non-Eusauropoda sauropods.

Vulcanodon karibaensis was, until recently, the earliest known sauropod and is one of the most basal species of this taxon. Originally considered a prosauropod, based on the partial skeleton found in Zimbabwe (Raath 1972), *V. karibensis* reveals relatively long forelimbs and supportive *manus*, conditions that allow inference of quadrupedal locomotion (Cooper 1984) and already reveals an increase in size, emblematic of more derived sauropods.

The species *Tazoudasaurus naimi* (pers. obs. 2006) is one of the most complete non-eusauropod available. Along with ‘*Cetiosaurus*’ *mogrebiensis* (Lapparent 1955) and *Atlasaurus imelakei* (Monbaron 1999)*, T. naimi* represents the sauropod fauna of the Early Jurassic of Morocco. Phylogenetically, *T. naimi* represents, with *Vulcanodon*, the sister group of Eusauropoda (Allain et al. 2004).

*Gongxianosaurus shibeiensis***,** like other basal sauropods, does not exhibit most of its cranial or axial skeleton, its phylogenetic positioning thus predominantely relying on the appendicular skeleton synapormorphies. This large sauropod of the Early Jurassic, despite its uncertain phylogenetic placement (Upchurch et al. 2004),

was positioned as follows: “The combination of characters (…) currently suggests that it was a non-eusauropod more derived than *Chinshakiangosaurus*…” (Barrett and Upchurch 2007, p. 107).

Category C2. NON-NEOSAUROPOD EUSAUROPODA UPCHURCH 1995

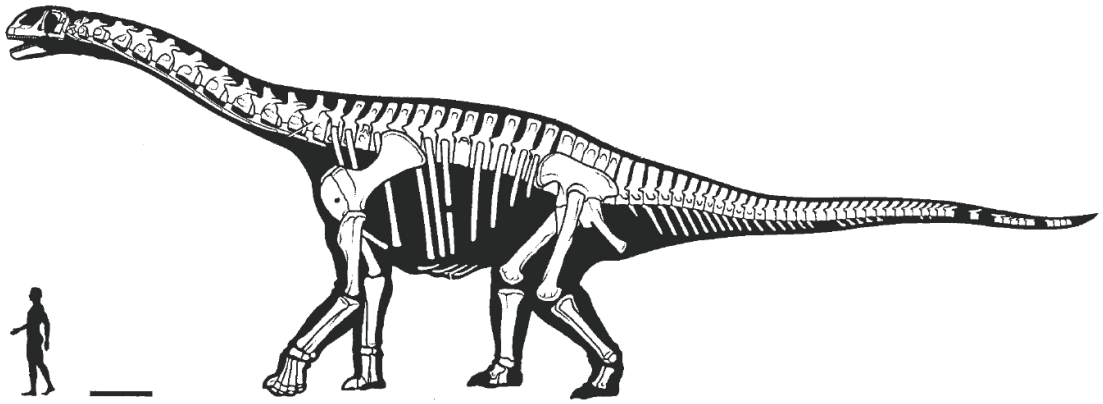

Figure 4.10 *Jobaria tiguidensis* skeleton reconstruction with preserved elements (adapted from Sereno et al. 1999). Scale bar 1 m.

Specimens included in this group: *Barapasaurus tagorei* Jain et al. 1975*; Cetiosauriscus stewarti* Charig 1980, 1993*; Cetiosaurus mogrebiensis* Lapparent 1955*; Cetiosaurus oxoniensis* Phillips 1871 (pers. obs. 2007‡)*; Datousaurus bashanensis* Dong and Tang 1984*; Ferganasaurus verzilini* Alifanov and Averianov 2003*; Hudiesaurus sinojapanorum* Dong 1997*; Jobaria tiguidensis* Sereno et al. 1999*; Klamelisaurus gobiensis* Zhao 1993*; Mamenchisaurus constructus* Young 1954; *Mamenchisaurus guangyuanensis* (pers.obs. 2006)*; Mamenchisaurus hochuanensis* Young and Zhao 1972 (pers.obs. 2006)*; Omeisaurus tianfuensis* He et al. 1984 (pers.obs. 2006)*; Patagosaurus fariasi* Bonaparte 1979 (pers.obs. 2005); *Shunosaurus lii* Zhang 1988 (pers.obs. 2006)*; Tehuelchesaurus benitezii* Rich et al. 1999*; Turiasaurus riodevensis* Royo-Torres 2006*; Volkheimeria chubutensis* Bonaparte 1979*; Yuanmousaurus jiangyiensis* Lu et al. 2006.

Barapasaurus tagorei was recently considered as a non-eusauropod sauropod (Upchurch et al. 2007), while the “traditional” inclusion of this species from

‡ The specimen observed in BMNH of *Cetiosaurus oxoninensis* is a plaster cast, non-numered and which has written on it “master cast”, of the original specimen housed in the Oxford Museum, described and figured by Phillips in 1871.

the Early Jurassic of Kota Formation of India in Eusauropoda has been favoured herein (Wilson 2002; Upchurch et al. 2004).

It was suggested that *Patagosaurus fariasi* (pers. obs. 2005) lies outside Eusauropoda, in a less derived position, along with *Barapasaurus tagorei* (Upchurch 1998). Posterior analysis of this Argentinean species included it in Eusauropoda, in a basal position, and considered it less derived than neosauropods (Wilson 2002).

The various species of the Chinese genus *Mamenchisaurus* Young 1954 included in this work all belong to Euhelopodidae (Upchurch 1995; Upchurch et al. 2004) and include: *Mamenchisaurus constructus, Mamenchisaurus hochuanensis* (pers. obs. 2007) and *Mamenchisaurus guangyuanensis* (pers. obs. 2007). The species *M. guangyuanensis* was formally erected and is most probably a juvenile form, due basically to its small size, incomplete fusion of vertebral elements and texture of articular surface of limb bones (pers. obs. 2007). Although Euhelopodidae was not herein adopted as a group, it is generally accepted that *Mamenchisaurus* is a non-neosauropod (Upchurch 1995, 1998; Wilson 2002).

Together with *Mamenchisaurus*, the large Chinese species *Omeisaurus tianfuensis* (pers. obs. 2007) and *Shunosaurus lii* (pers. obs. 2007) constitute a controversial area of sauropod phylogeny, that is to say, involved in the debate over the hypothetical monophyly (Upchurch 1995, 1998) or paraphyly (Wilson and Sereno 1998; Wilson 2002) of Euhelopodidae. The paraphyletic proposal suggests *Omeisaurus* to be “occupying the sister-taxon to Neosauropoda (…), but *Shunosaurus* positioned basally and *Euhelopus* positioned apically.” (Wilson 2005a, p. 18).

Cetiosauriscus stewarti was until recently considered a member of Diplodocoidea (Charig 1980; Upchurch et al. 2004), based on elements of the axial and appendicular skeleton. Different analyses proposed that *C. stewarti* should be part of a clade that included *Mamenchisaurus* and *Omeisaurus* (Rauhut et al. 2005, fig. 2).

Another member of Euhelopodidae is the recently described Chinese sauropod *Yuanmousaurus jiangyiensis*, considered more primitive than *Euhelopus,* but more derived than *Omeisaurus* (Lu et al. 2006).

'Cetiosaurus' mogrebiensis, despite being considered a *nomem dubium* (Upchurch and Martin 2002, 2003) is herein integrated in the original phylogenetic proposal (Cetiosauridae). The only valid species of *Cetiosaurus* is *C. oxoniensis* (Upchurch and Martin 2002, 2003), from the Middle Jurassic material of England.

Hudiesaurus sinojapanorum (pers. obs. 2007) was included in Mamenchisauridae. *H. sinojapanorum* is not included in any of the main phylognetic proposals used in this work (e.g., Upchurch 1998; Wilson 2002). Therefore, the proposal of the original descriptors of this Chinese material has been herein adopted.

Turiasaurus riodevensis is the biggest European sauropod from the Jurassic-Cretaceous sediments of Spain and allowed its describers to erect a new taxon – Turiasauria – with the most derived placement within Eusauropoda (Royo-Torres 2006, fig. 3).

Klamelisaurus gobiensis was proposed by the original author as a member of the family Brachiosauridae. Later, with the phylogenetic analyses of the 1990's, *K. gobiensis* was related to *Omeisaurus*, *Mamenchisaurus* and *Euhelopus* (Upchurch 1995).

Jobaria tiguidensis was regarded as a Macronaria (Upchurch et al. 2004) but it was decided, on basis of both the original description and the posterior analysis, to consider it as a neosauropod outgroup (Sereno et al. 1999; Wilson 2002, fig. 1.4; Royo-Torres et al. 2006, fig. 3).

Datousaurus bashanensis was assigned to Euhelopodidae, similar to other Chinese specimens (*Shunosaurus* and *Omeisaurus*) from the Dashanpu quarry of Zigong (Upchurch 1995).

Tehuelchesaurus benitezii was regarded as an omeisaurid (Rich et al. 1999; Upchurch et al. 2004, fig. 13.18), due to its morphological similarities with that Chinese fauna.

Volkheimeria chubutensis is the most basal representative of the non-neosauropod, along with *Patagosaurus* (Bonaparte 1986a, b, 1999; Wilson 2002; Upchurch et al. 2004).

Ferganasaurus verzilini is considered as a neosauropod by the original description work (fig. 17) and by other authors (Royo-Torres 2006, supporting material). The incorporation of *F. verzilini* in non-neosauropod group presented some methodological problems. Neosauropoda comprises *Diplodocoidea* and *Titanosauria* (Wilson 2005aa, p. 27), but could not integrate *F. verzilini*, since this work does not include a "non-diplodocoid neosauropod" group. Therefore, it has been decided to place *F. verzilini* in the non-neosauropod group, despite the phylogenetic contradiction of this option.

Category D. DIPLODOCOIDEA MARSH 1884; UPCHURCH 1995

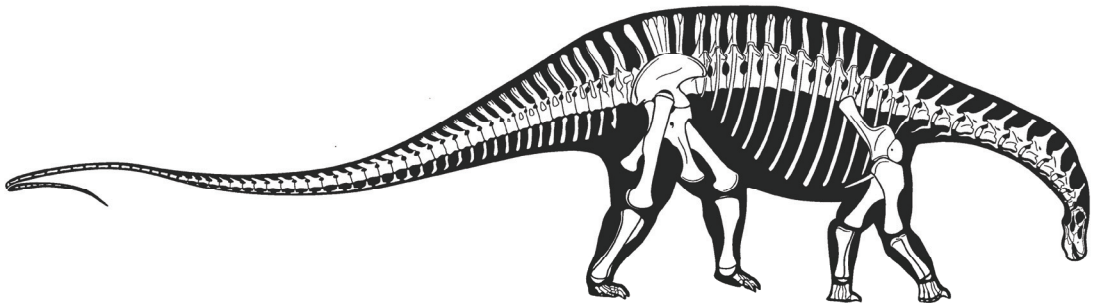

Figure 4.11 *Dicraeosaurus hansemanni* silhouette skeletal reconstruction. Adapted from Wilson 2002.

Specimens included in this group: *Amargasaurus cazaui* Salgado and Bonaparte 1991 (pers.obs. 2005)*; Apatosaurus ajax* Marsh 1877*; Apatosaurus excelsus* Gilmore 1936 (pers.obs. 2005)*; Apatosaurus louisae* Holland 1915 (pers.obs. 2005)*; Apatosaurus sp.; Apatosaurus (Eobrontosaurus* Bakker 1998*) yahnahpin* Filla and Redman 1994*; Apatosaurus alenquerensis (=Camarasarus alenquerensis)* Lapparent and Zbyszewski 1957*; "Barosaurus" africanus* Janensch 1922 (pers.obs. 2006)*; Barosaurus lentus* Marsh 1890; *Dicraeosaurus hansemanni* Janensch 1914 (pers. obs. 2006)*; Dicraeosaurus sattleri* Janensch 1914

(pers. obs. 2006); *Diplodocus carnegii* Hatcher 1901 (pers.obs. 2005)*; Diplodocus hayi* Holland 1924*; Diplodocus longus* Marsh 1878 (pers.obs. 2005)*; Diplodocus sp.*; *Haplocanthosaurus sp.* Hatcher 1903*; Rebbachisaurus tessonei* Calvo and Salgado 1995 (pers.obs. 2005)*; Suuwassea emilieae* Harris and Dodson 2004; *Tornieria africana* Fraas 1908 (pers.obs. 2006).

Diplodocoidea is one of the two constituent lineages of Neosauropoda, along with Macronaria (Salgado et al. 1997a; Upchurch 1998; Wilson and Sereno 1998; Wilson 2002; Taylor and Naish 2005), and integrates diplodocoids such as the basal *Haplocanthosaurus* (Calvo and Salgado 1995) and the more derived *Diplodocus*. It was decided to adopt Wilson (2002) position for the genus *Haplocanthosaurus* as a diplodocoid, although recent phylogenetic analysis (Upchurch et al. 2004, fig. 13.18) placed it in Macronaria, closer to Titanosauria than *Camarasaurus*.

Suuwassea emilieae is a recently described taxon from the Morrison Formation with mixed morphological features, from both diplodocids and dicraeosaurids (Harris and Dodson 2004; Harris 2006a, b, c).

The relatively short-necked *Dicraeosaurus hansemanni* and *Dicraeosaurus sattleri* are original from the Tendaguru basin in Tanzania. Both species belong to Dicraeosauridae Janensch 1929 and offer several specimens, skull and postcranial material.

Evolutionarily closely related to *Dicraeosaurus* (Upchurch et al. 2004; Wilson 2002) is the Argentinean sauropod *Amargasaurus cazaui*, that possesses caractheristic long bifid neural spines.

The revision of the material attributed to *Rebbachisaurus tessonei* allows proposing that this material should be assigned to *Rayososaurus agrioensis* (Wilson and Sereno 1998). More recent works updated the taxonomy for *R. agrioensis* and named this taxon as *Limaysaurus tessonei* (Salgado et al. 2004), a nomenclature also used in this work for material previously described as *R. tessonei*.

The long known genus *Apatosaurus* Marsh 1877 includes several nearly complete specimens and species such as *Apatosaurus ajax*, *Apatosaurus excelsus*, *Apatosaurus louisae*, *Apatosaurus sp.*, *Apatosaurus* (*Eobrontosaurus* Bakker 1998) *yahnahpin*, all from distinct areas of the Morrison Formation. *Apatosaurus alenquerensis* from the Upper Jurassic of Portugal was originally attributed to *Camarasaurus alenquerensis*. Posterior reevaluation of the material considered the former species as *A. alenquerensis* (Mcintosh 1990, 1996).

Diplodocus longus, *Diplodocus carnegii*, *Diplodocus hayi* and *Diplodocus sp.* are, similarly to Apatosaurus, species from the Morrison Formation with a well known anatomy and phylogenetical location.

Tornieria africana, another species from Tendaguru, was recently reevaluated and thereby differentiated from other species of *Barosaurus* (Remes 2004, 2006), namely *'Barosaurus' africanus*, and is a sister taxon of the unnamed node *Barosaurus*+*Diplodocus* (Remes 2006, pag.664, fig. 9).

The species *'Barosaurus' africanus* and *Barosaurus lentus* come from the Tendaguru basin and from the Morrison Formation, respectively. Part of '*B'. africanus* material that could be observed in the MB is now considered as *Tornieria africana* (Remes 2006, Appendix 1). The material that has not been incorporated in the referred revision work has been considered as in the original description works and integrating Barosaurus.

Category E1. (BASAL) MACRONARIA WILSON AND SERENO 1998

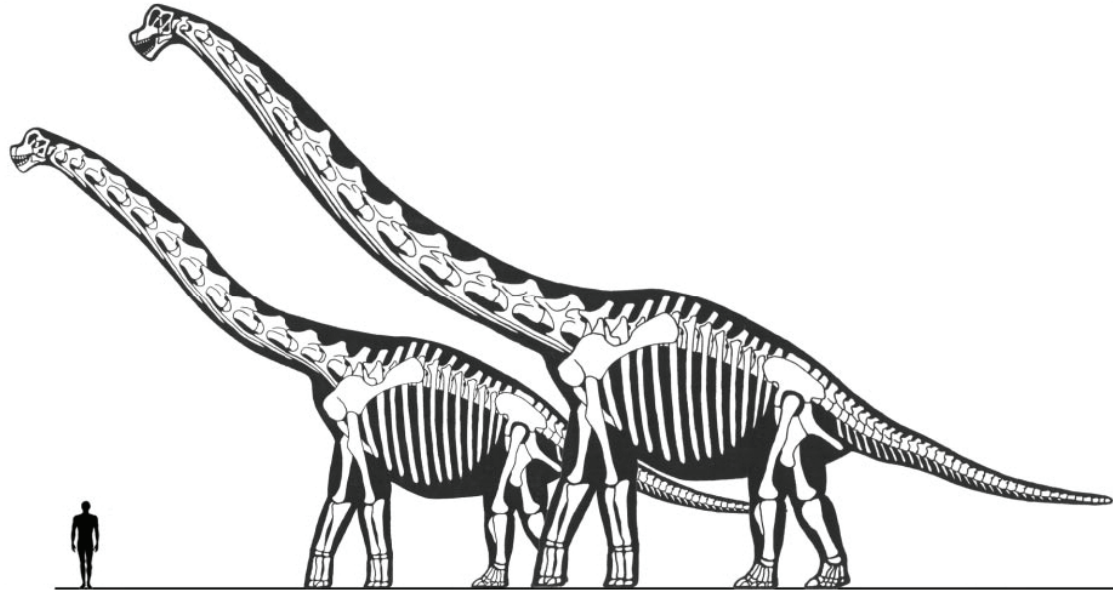

Figure 4.12 Silhouette skeletal reconstructions and comparison of *Brachiosaurus brancai* and *Sauroposeidon proteles*. The reconstruction of *Sauroposeidon proteles* (right) is hypothetical, based on the skeleton of *Brachiosaurus brancai* after the HM SII specimen. Adapted from Wedel et al. 2000. Human figure is 1.8 m high.

Specimens included in this group: *"Pelorosaurus" becklesi* Mantell 1852*; Bellusaurus sui* Dong 1990 (pers. obs. 2006)*; Bothriospondylus madagascariensis* Lydekker 1895*; Brachiosaurus altithorax* Riggs 1903*; Brachiosaurus brancai* Janensch 1914 (pers.obs. 2006)*; 'Brachiosaurus' ataialensis* [§] Lapparent and Zbyszewski 1957; *Camarasarus sp.*; *Camarasaurus grandis* Marsh 1877*; Camarasaurus lentus* Marsh 1889 (pers.obs. 2005).*; Camarasaurus supremus* Marsh 1877*; Euhelopus zdanskyi; Erketu ellisoni* Ksepka and Norell 2006.

'Pelorosaurus becklesi' is a titanosaurid from the Lower Cretaceous of England known by forelimb material and skin impressions (Upchurch 1995; Upchurch et al. 2004).

Brachiosaurus altithorax, Brachiosaurus brancai, *'Brachiosaurus' ataialensis* all belong to Brachiosauridae Riggs 1904, which is defined as "Titanosauriforms more closely related to *Brachiosaurus* than to *Saltasaurus,* including, by this definition, the French *'Bothriospondylus' madagascarensis* (i.e., not the material from Madagascar),

[§] *'Brachiosaurus' ataialensis* was recently (Antunes and Mateus 2003) attributed to *Lusotitan atalaiensis* Lapparent and Zbyszewski 1957. In this work we maintain the previously nomenclature due the absence of any phylogenetic hypothesis that propose a *Brachiosauridae* ingroup relationships with *L. atalaiensis*.

Brachiosaurus, Eucamerotus, and *Pleurocoelus.*" (Wilson and Sereno 1998, pp. 20-21). These sauropods, from the Morrison and Tendaguru Upper Jurassic basins, exhibit some anatomical peculiarities, namely the relatively long neck, greatly elongated fore limbs, longer than the hind limbs, and columnar *manus*.

The genus Camarasaurus Cope 1877 comprises several species and was circumscribed as "*C. grandis, C. lentus, C. lewisi, C. supremus,* their ancestor, and all its descendants." (Wilson and Sereno 1998, p. 20).

Erketu ellisoni belongs to Somphospondyli (Wilson and Sereno 1998), which is a clade not adopted in this work. Therefore, the closest group appropriate for this specimen, and respecting the adopted classification coherency, is to consider *E. ellisoni* as a basal macronarian for the purposes of this study.

Euhelopus zdanskyi Wiman 1929 is an Early Cretaceous sauropod from China. Several phylogenetic analyses placed *E. zdanskyi* in the monophyletic radiation Euhelopodidae (e.g. Upchurch 1995), that is to say, considered it as a non-neosauropod. Other classifications placed *E. zdanskyi* in a more derived positioning within Macronaria or in Titanosauria level (Wilson and Sereno 1998; Curry-Rogers and Foster 2001; Wilson 2002; Ksepka and Norell 2006). This work assumed the Macronaria positioning for *E. zdanskyi*.

Bothriospondylus madagascariensis was attributed to Brachiosaurus (Wilson 2002, table 13).

Bellusaurus sui is a sauropod from the middle Late Jurassic of China and considered to be a juvenile macronarian (Upchurch et al. 2004, fig. 13.18).

Category E2. (BASAL) TITANOSAURIA BONAPARTE AND CORIA 1993

Specimens included in this group: *Aegyptosaurus baharijensis* Stromer 1932; *Andesaurus delgadoi* Calvo and Bonaparte 1991; *Argyrosaurus superbus* Lydekker 1893 *Chubutisaurus insignis* Del Corro, 1975 (pers.obs. 2005); *Epachthosaurus sciuttoi* Powell 1990; *Gobititan shenzhouensis* You et al. 2003;

Janenschia robusta Wild 1991 (pers.obs. 2006) was previously *Tornieria robusta*; *Venenosaurus dicrocei* (Tidwell et al., 2001).

The descriptions of the species belonging to Titanosauria and Lithostrotia are condensed, opposite to what was done, for example, in non-titanosaur sauropods, due fundamentally to the general agreement in the phylogeny of Titanosauria and Lithostrotia. The species included in both Titanosauria and Lithostrotia are summarized in figure 4.14.

Despite the numerous phylogenetic analyses on the Titanosauria radiation and its interrelationships executed in the last decade, proposing some classification stability in this and the derived clades (e.g., Upchurch 1995, 1998; Salgado et al. 1997a; Sanz et al. 1999; Wilson and Upchurch 2003; Calvo and Gonzalez-Riga 2003; Upchurch et al. 2004; Curry-Rogers 2005), the recent comprehensive analysis was favoured (Wilson 2006, fig. 2).

Category E3. LITHOSTROTIA UPCHURCH ET AL. 2004

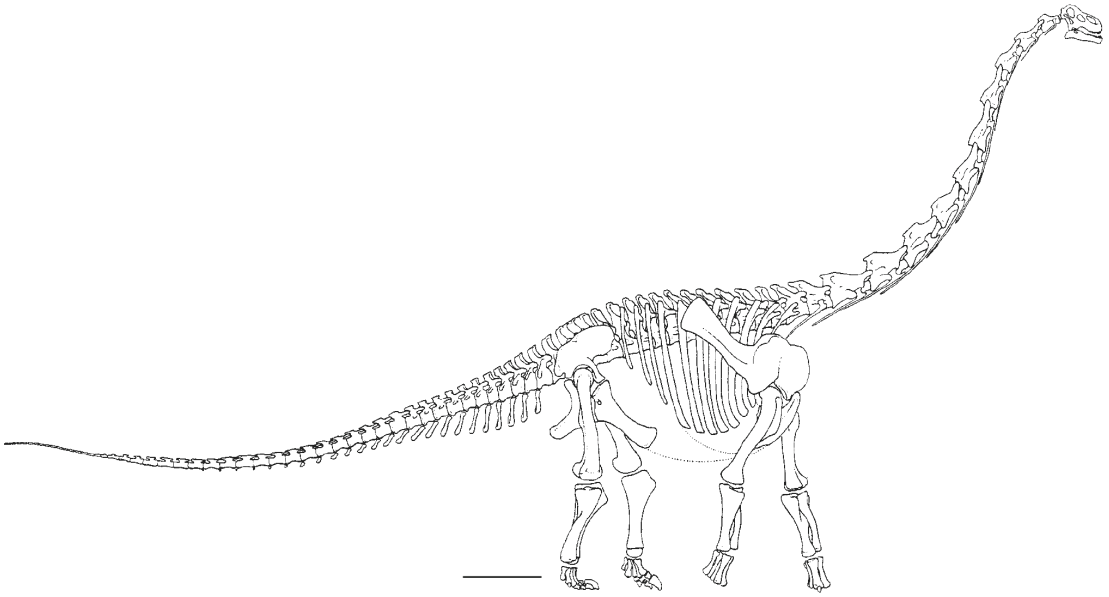

Figure 4.13 *Alamosaurus sanjuanensis* skeletal reconstruction (adapted from Lehman and Coulson 2002). Note the columnar hands. Scale bar 1 meter.

Specimens included in this group: *Aeolosaurus rionegrinus* Powell 1987 (pers.obs. 2005); *Agustinia ligabuei* Bonaparte 1999a; *Alamosaurus sanjuanensis* Gilmore 1922; *Antarctosaurus wichmannianus* Huene 1929; *Laplatasaurus araukanicus* Huene 1929[**] (pers.obs. 2005); *Ligabuesaurus leanzai* Bonaparte et al. 2006; *Neuquensaurus australis* Powell 1987 (pers.obs. 2005); *Opisthocoelicaudia skarzynskii* Borsuk-Bialynicka 1977*; Rapetosaurus krausei* Curry-Rogers and Forster 2001; *Saltasaurus loricatus* Bonaparte and Powell 1980, 1992 (pers.obs. 2005).

Lithostrotia monophyly is well supported (Curry-Rogers 2005) and this group was selected in order to separate the more derived forms of the titanosaur radiation from the basal titanosauria forms.

Alamosaurus sanjuanensis is an Upper Cretaceous lithostrotian from various North-American sites (Upchurch et al. 2004). A juvenile specimen of *A. sanjuanensis* was recently described (Lehman and Coulson 2002) and the similarities to other titanosaurids (the unnamed titanosaur from Peiropolis - Brazil and *Neuquensaurus australis* from Argentina) allowed some paleogeographical inferences.

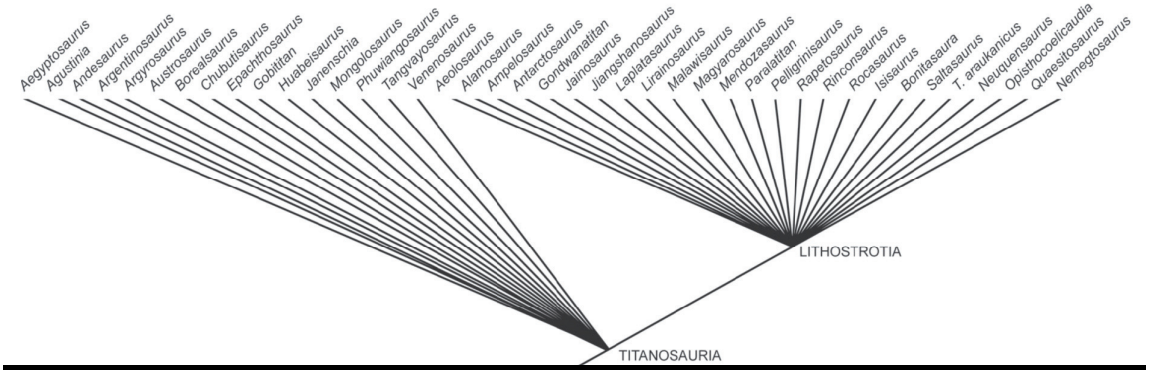

Figure 4.14 Phylogenetic distribution of Titanosauria and Lithostrotia sauropods. Adapted from Wilson (2006, fig. 2).

Antarctosaurus wichmannianus was described on basis of partial cranial and appendicular skeleton from the Rio Negro Formation. This massive sauropod genus was considered a *Titanosauria* (Curry-Rogers and Forster 2001, fig. 4[††]; Salgado &

[**] "Powell's (1986) unpublished thesis remains the most recent treatment of South American titanosaurs. Like that of Huene (1929), Powell's work included description of new taxa based on recent discoveries (*Aeolosaurus*, *Epachthosaurus*) and revision of the taxonomy of his predecessors – transferring *T. australis* and *T. robustus* to a new genus (*Neuquensaurus*) andreferring Huene's *Laplatasaurus araukanicus* back to *Titanosaurus*." (Wilson and Upchurch 2003, p.139).

[††] The species of *Antarctosaurus* in the referred phylogenetic analysis is *A. septentrionalis*.

Calvo 1997) or a member of Diplodocoidea (Upchurch 1999), but the recent revision analysis (Wilson 2006, fig. 2), which places *A. wichmannianus* in Lithostrotia, was favoured.

Opisthocoelicaudia skarzynskii was interpreted as a camarasaurid (Borsuk-Bialynicka, 1977; McIntosh, 1990) but is currently regarded as an element of Titanosauroidea (Upchurch 1995).

Saltasaurus loricatus (=*Titanosaurus robustus* Upchurch et al. 2004) was identified by cranium, axial and appendicular skeleton remains of at least five individuals from two provinces of Argentina (Bonaparte and Powell 1980; Powell 1992). The highly derived anatomical features of *S. loricatus* forced its use as an anchor taxon for most of the clades in the Sauropoda phylogeny.

Agustinia ligabuei (Bonaparte 1999b) is considered in this work as belonging to Lithostrotia (Curry-Rogers 2005, fig. 2.11.), despite its setting in Titanosauria depicted in figure 4.14 (Wilson 2006).

Laplatasaurus araukanicus, *Aeolosaurus rionegrinus*, *Neuquensaurus australis* and *Rapetosaurus krausei* are the remaining lithostrotians which phylogenetical positions are justified in Wilson (2006, fig. 2), although some of its internal relationships presently remain unsolved. This fact does not constitute a methodological obstacle to our work, as our main objectives are not phylogenetical directed.

Chapter 5 - Sauropodomorpha locomotion - evolutionary history and appendicular skeleton morphology

5.1 Sauropodomorph functional morphology - anatomical characteristics of the appendicular skeleton and locomotion patterns

- 5.1.1 Sauropodomorphs - bipedality vs quadrupedality
- 5.1.2 Sauropodomorphs - body-size and locomotion
- 5.1.3 Limb proportions as a locomotor indicator

5.2 Sauropodomorpha anatomical characteristics of the appendicular skeleton

- 5.2.1 Stylopodium
- Femur
- Humerus
- 5.2.2 Zeugopodium
- Tibia
- Radius
- Ulna
- 5.2.3 Autopodium
- Manus
- Pes

"The performance of an organism is the crucial link between its phenotype and its ecological success."

Koehl 1996

The present work aims, as stated in previous chapters, to explore limb morphological disparity, specifically among Sauropodomorpha, as well as to identify and improve the characterization of morphological changes occurred along this group's evolutionary history. In this chapter, an introduction to the evolution of locomotion of Sauropodomorpha will be given, as well as the description of several important morphological modifications in the appendicular skeleton that could be coupled with that process.

The morphological analyses performed in this work will make use of the phylogeny of Sauropodomorpha, which was introduced in chapter 4, in order to define an evolutionary framework within this group.

The inference of locomotor function in sauropodomorphs from the appendicular form is a challenging project in a research context where experimental methodology is inadequate in most of the situations - see further explanations.

5.1 Sauropodomorph functional morphology - anatomical characteristics of the appendicular skeleton and locomotion patterns

5.1.1 Sauropodomorpha - bipedality vs quadrupedality

Dinosaurs originated as small-sized, upright bipeds (e.g., Carrano 2000). Quadrupedalism in certain dinosaur groups replaced bipedalism. A series of intermediate 'semi-bipedal' taxa show apparent capability of using both postures - for example, hadrosaurs and prosauropods (Carrano 2001). In contrast to mammals, for which the primitive condition is quadrupedality, observable in the eutherian basal form *Eomaia* (Hu et al. 1997), bipedal locomotion appearing secondarily in some groups, obligate quadrupedalism in dinosaurs appeared independently in different dinosaur groups: Sauropoda, Thyreophora, and Ceratopsia (Sereno 1997).

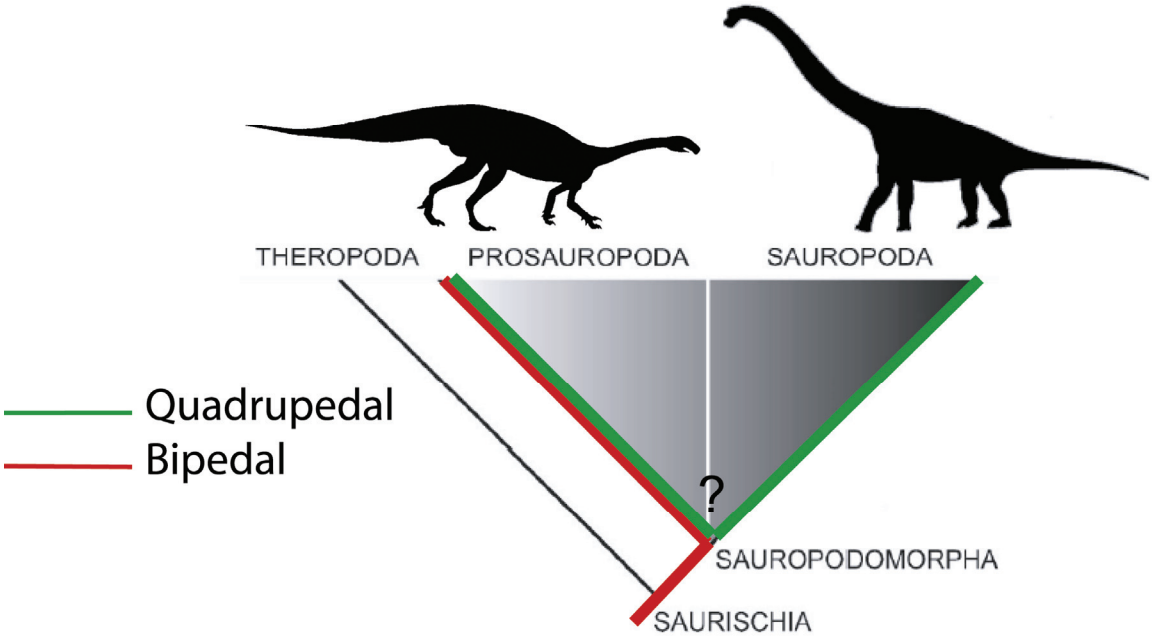

Figure 5.1 Simplified cladogram of Saurischia phylogenetic relationships and inferred types of locomotion. Adapted from Wilson 2005b (fig.1). Silhouettes of *Plateosaurus engelhardti* and *Brachiosaurus* based on Wilson and Sereno 1998 and Yates 2003b, respectively.

Thus in some taxa there is a gradation between bipedal and quadrupedal dinosaur locomotion, reflected in overlapping patterns of limb bone scaling (Carrano 2001) and morphology. For example, the characteristic sauropod graviportal limb posture was probably associated with a reduction of lower limb flexion and extension (Carrano 2005).

Non-sauropods sauropodomorphs have been traditionally interpreted as obligatory bipedals (e.g., Galton 1976, Galton and Upchurch 2004), due to several aspects of its appendicular and axial morphology: limb elements proportions (shorter fore limbs vs. longer hind limbs), elongated trunks and other morphological differences described in the following chapters.

Concerning the scaling of the long bones of sauropodomorphs, there seem to be similarities between bipedal and quadrupedal hind limb bones (Carrano 2001). This fact was interpreted as a consequence of evolutionary conditions involved in the development of quadrupedalism in dinosaurs (Carrano 2001) and the scaling

differences among bipedal and quadrupedal sauropodomorphs, such as lower curvature and greater eccentricity, the result of animal size changes.

Figure 5.1 illustrates, as seen, one of the most important aspects of sauropodomorph evolutionary history - the appearance of secondary quadrupedality in Sauropodomorpha.

Despite comprising some of the largest terrestrial vertebrates that ever lived on Earth, the fact remains that sauropodomorphs internal relationships are not fully understood, particularly regarding basal forms, as stated in the previous chapter. These phylogenetic ambiguities could have functional and postural implications in the evolutionary study of the morphology of appendicular skeleton, like the present one. However, the methodological uncertainties have been minimized in this work through the use of the most updated relationships among this group.

Although the phylogenetical incertitude of certain sauropodomorph groups could be reduced, there is also one obvious pragmatic difficulty that arises in any sauropodomorph locomotor study, namely the inexistence of adequate phylogenetical extant models. Traditionally, distinct groups of animals served as biological models/analogues for sauropod locomotion, such as the Proboscidea (elephants and extinct relatives), Xenarthra (large ground sloths) and Dinocerata (uintatheres) - e.g. Holland 1910; Bakker 1971; Alexander 1976; Coombs 1978; Christiansen 1997; Henderson 2006. These biological groups were used since they present massive body mass and relatively appendicular morphological alikeness with those extinct archosaurs, despite the large phylogenetical and temporal gap between them.

In contrast, studies dealing with theropod locomotion frequently use crocodiles and/or birds as living models/analogues in order to infer postures, biomechanical constrains or locomotor behavior (e.g., Paul 1998; Carrano and Biewener 1999), despite the changes that occurred during avian evolution, specifically alterations in limb

morphology. Aves reveal the necessary phylogenetical proximity to theropod dinosaurs which allows validating biomechanical conclusions in a phylogenetic framework.

5.1.2 Sauropodomorphs - body-size and locomotion

Body-size is an important factor in understanding macroevolutionary patterns of the appendicular skeleton transformations in Sauropodomorpha. Two major aspects of the sauropodomorphs paleobiology are directly associated with morphological changes in the appendicular skeleton (Wilson and Carrano 1999; Carrano 2001): the massive body-sizes reached by most of the species of this group; and the changes in posture and locomotion along its evolutionary history, from a primitive bipedal stance to a derived quadrupedal one.

The mentioned biological questions are intimately associated in a bidirectional path, since locomotor modifications could have implied the evolutionary adaptation of size increase and/or gigantism may have implied morphological changes in the locomotor apparatus.

Gould and MacFadden (2004), authors which introduced the concepts of Autapomorphic Giantism and Phyletic Giantism, will be followed herein.[*] One could define autapomorphic giantism whenever “body-size increase occurs on a single branch within a clade” and phyletic giantism when “successive body-size increase occurs in nested clades within a lineage.” (Gould and MacFadden 2004, p. 220).

The higher-level trend for increasing body-size along the Sauropoda – phyletic gigantism, is traditionally referred, as are some exceptions: neosauropod members reveal different size limits and trends among the two constituent lineages – Diplodocoidea and Macronaria. Based on the data compiled in table 5.1, both upper and lower body mass limits of macronarians are more extreme than in diplodocoids,

[*] In this work the term *gigantism* will be favoured despite the preference of the cited authors for *giantism*: “The terms *giantism* and *nanism* are preferred here rather than the frequently, although incorrectly used equivalents, gigantism and dwarfism, respectively.” (Gould and MacFadden 2004, p. 219)

that is to say, macronarians present extremer species in terms of body mass, since this group includes species with high and low body masses.

In spite of absolute differences in body mass estimates, one could state that there is a phyletic gigantism along the Sauropoda clade. This fact does not invalidate the relative size decrease observed within some clades of Sauropoda, explicitly in macronarians, or even the existence of non-sauropods heavier than derived sauropods (e.g., *Coloradisaurus brevis*).

The cited tendency for size increase could be assumed for non-sauropod sauropodomorphs, since more derived forms present similar body masses to basal sauropods. The problems arises with the focus within clades, since most of the internal relationships of the groups are not quite well established. Despite this, there are some morphological tendencies in the appendicular skeleton of Sauropodomorpha.

Basal Sauropodomorpha	Plateosauria	Sauropodiformes	non-Eusauropoda	non-Neosauropoda	Diplodocoidea	basal Macronaria	Titanosauria	Lithostrotia
Thecodonto. 0.07-01[g]	*Plateo.* 1[c] 2.1[d] 0.63-0.91[e] 1-4[g] *Lufengo.* 1-4[g] *Rioja.* 1-4[g] *Massospon.* 0.1-0.4[g]	*Anchi.* 0.01-0.04[g] *Euskelo.* 1-4[g] *Melanoro.* 1-4[g]	*Vulcanodon* 10-40[g]	*Barapa.* 10-40[g] *Mamenchi.* 15.1[b] 10-40[g] *Patago.* 10-40[g] *Shuno.* 3.6[b] 7-10[g]	*Amarga.* 5-10[a] 2.6[b] 10-40[g] *Apato.* 20.6[b] 34[f] 10-40[g] *Dicraeo.* 5-10[a] 5.7[b] 10-40[g] *Diplodo.* 16[b] 10-40[g]	*Argentino.** 50[a] 73[b] *Camara.* 9.3[b] 10-40[g] *Brachio.* 39.5[b] 37[f] 10-40[g]	*Chubuti.* 10-40[g] *Ande.* 40-70[g]	*Antarcto.* 40-70[g] *Neuquen.* 1.5-3[a] *Opistho.* 8.4[b] 10-40[g] *Salta.* 3[a] 7-10[g]

Table 5.1 *Sauropodomorpha* estimated body masses (in tons). Data from: a – Carrano 2005; b – Mazzetta et al. 2004; c – Seebacher 2001; d - Sander 1992; e – Gunga et al. 2007; f – Christiansen 1997; g – Peczkis 1994. * Specimen not included in this work

Gigantism observed in some lineages of Sauropodomorpha, especially in *Sauropoda*, implies morphological modifications in the appendicular skeleton that are associated to the development of secondarily quadrupedality. Some of these anatomical features were previously identified by several authors (Carrano 1998, 2000,

2001, 2005; Christiansen 1998; Wilson 1998, 2002; Wilson and Carrano 1999; Hutchinson and Gatesy 2000; Bonnan 2003) and include:

- columnar, graviportal limb posture;
- increased limb robusticity;
- shortened distal limb segments;
- increased femoral midshaft eccentricity.

Columnar limb shafts were also recognized in non-sauropods as *Riojasaurus incertus* (pers. obs. 2005) and *Melanorosaurus readi*, allowing the establishment of a close relationship between those two forms (Sereno 2007). This fact corroborates the relationship between femoral curvature and size, as *R. incertus* and *M. readi* are among the larger prosauropod species known.

The columnar stance arose by size increase may have originated the reduction in distal limb segments (Carrano 2001, 2005), with consequent functional implications on the lower limb flexion and torsion.

Theropods and prosauropods present sigmoid femora, oppositely to what is observed in sauropods, which typically present straight bones – figure 5.2, numbers 1-2 and 6, figure 5.3, number 4. A more columnar femoral shaft permits bigger resistance to bigger body masses as those of the sauropods (Carrano 2001).

Femoral eccentricity seems to be related with size increase in sauropods, as well as in other groups of dinosaurs, and this design was interpreted as a means to increase resistance to mediolateral bending on parasagittal bones (Carrano 2001).

5.1.3 Limb proportions as a locomotor indicator

An introductory revision of the diversity of compositional data used in locomotor studies regarding sauropodomorphs, as well as some of its methodological insufficiencies, was given in detail at the second and third chapters and will be applied in various groups of dinosaurs, with special emphasis on sauropodomorphs, and on some specific groups of mammals.

Relative proportions of each limb element, as well as among fore and hind limbs, have been long used as a locomotor indicators (e.g. Galton 1976, Coombs 1978). The common limb ratios in dinosaurian locomotor analyses focus on numerous combinations of the possible lengths between the limb bones and frequently include ratios such as are the fore limb vs. hind limb; femur vs. tibia; metatarsal III vs. tibia, among many others. The referred examples of ratios were also analyzed in combination with axial skeleton morphometric data like the trunk length (e.g., Galton 1976).

There are numerous tables/figures that compile and use appendicular elements compositional data and/or ratios in dinosaur locomotor studies (e.g., Coombs 1978, figures 8 and 9; Christiansen and Bond, 2002, fig. 3; Bonnan and Senter 2007, tables 1 and 2) which are the materialization of the importance attributed to compositional data in this context.

Despite the long and extensive use of this sort of morphometric data, no new quantitative approaches have been introduced recently. Similarly, the concept of evolutionary module in an appendicular skeleton context has been neglected, unnoticed or, more plausibly, difficult to identify. Regarding each of the limb elements as a unit of a biomechanical system never surpassed the “more distal” or “more proximal” categorization – recall the concept of modularity introduced in chapter 1.

Coombs (1978) estimated the locomotor capabilities of dinosaurs by comparing plots of hind limb proportions (tibia vs. femur/metatarsal III vs. tibia) with those of living mammals, in order to establish several locomotor categories. Although a specifically directed reevaluation of these indices has not been performed, it should be mentioned that they are affected by the "spurious correlation", which affects most of the compositional data - recall chapters 2 and 3.

Pearson (1897) warned "*Beware of attempts to interpret correlations between ratios whose numerators and denominators contain common parts*." Coombs only plotted these ratios and no statistical analyses were carried out. More recently, other authors have performed similar ratios analysis containing common parts - e.g. hind limb proportions in avian and non-avian theropods, using tibia vs. femur/ metatarsus vs. tibia ratios (Christiansen and Bond, 2002, fig. 3).

Based on the referred Coombs categories, small- to medium-sized prosauropods, such as *Ammosaurus*, *Anchisaurus*, *Massospondylus*, *Saturnalia*, *Sellosaurus*, and *Thecodontosaurus* were classified as low-grade subcursorial runners. Large prosauropods, such as *Jingshanosaurus*, *Lufengosaurus*, *Melanorosaurus*, *Plateosaurus*, and *Yunnanosaurus* were included in the mediportal group. This author also refers that prosauropods were probably the slowest of the bipedal dinosaurs, but better runners than most other quadrupedal dinosaurs (Coombs 1978).

Some of the appendicular morphological features in sauropodomorphs that were identified and linked with the locomotor and postural changes in the evolutionary history of this group will be described below.

5.2 Sauropodomorpha anatomical characteristics of the appendicular skeleton

5.2.1 Stylopodium (the most proximal element of the tetrapod limb, including the humerus and femur)

Femur

The proximal hind limb bone reveals several morphological deviations along the sauropodomorph evolutionary history. Sauropod femora are anteroposteriorly flattened, revealing an elliptical shaft (McIntosh 1990; Wilson and Sereno 1998) which is synapomorphic for this group (Wilson and Sereno 1998) and does not exhibit the sigmoid curvature present in prosauropods and theropods. This morphology of sauropods is related fundamentally to its higher mass, which requires a more columnar bone and, therefore, all sauropods present straight and columnar femora (McIntosh 1990).

Another morphological change in sauropodomorph femora is implicated with the relative shape and position of the femoral fourth trochanter. The fourth trochanter is the area of insertion for the *caudofemoralis longus* and *caudofemoralis brevis* muscles (Romer 1956) and it has been demonstrated that, in dinosaurs, both the size and prominence of the fourth trochanter are indicators of the size and contribution of the *caudofemoralis longus* to the retraction of the femur during locomotion (Gatesy 1990, 1995). The closer the fourth trochanter is located to the femoral head, the more the lower part of the femur can swing and, consequently, improve the speed originated by that movement (Hildebrand, 1995). Bonnan (2004, pp. 464-465) stated that “The more distally placed the fourth trochanter is from the femoral head, the greater the turning moment of the femoral shaft about the femoral head becomes while simultaneously decreasing the arc of femoral retraction (…)”.

A more distal fourth trochanter implies, therefore, a greater retraction force at the cost of speed. Usually, the fourth trochanter in bipedal dinosaurs (or presumably bipedals) is located on the posterior face of the femur, in its proximal third – figure 5.2, numbers 1-5.

This condition changes in heavy-built sauropods to a more distal positioning of the fourth trochanter, near half-length - figures 5.2 and 5.3. Since the fourth trochanter positioning is related to the location of the caudofemoral muscle insertion (Romer 1956; Gatesy 1990, 1995, 1997), this topological criterion has been used as an indicator of the efficiency of locomotion in sauropods.

The basal theropod *Herrerasaurus* has a posteriorly directed fourth trochanter and, similar to prosauropods, a posterior *sulcus* in the proximal articular surface that is closer to the femoral head than in sauropods - figures 5.2. and 5.5. The fourth trochanter in prosauropods is more curved and "higher" than in sauropods, with a flat surface and a steep distal margin: for example, *Lufengosaurus*, *Yunnanosaurus* - figure 5.3, numbers 1-2 and 5; pers. obs. This morphology is used as character (140) in basal sauropodomorphs phylogenies (Yates 2003).

The proximal articular surface in *Herrerasaurus* is expanded anteroposteriorly, morphologically similar to what can be observed in prosauropods. Non-sauropod sauropodomorphs exhibit a femur with a shape very similar to other saurischians, namely theropods, with an anteroposterior curvature in lateral view and an anteromedially directed femoral head.

The femoral head is more expanded posteriorly in prosauropods and is not greatly expanded from the shaft (Galton and Upchurch 2004; pers. obs.) – figure 5.5. The femoral cross-section of prosauropods is sub-oval (Wilson and Sereno 1998) and the distal condyles are not as convex as in theropods.

Prosauropods exhibit sub-equal condyles with the anteroposterior length almost matching the lateromedial length – figure 5.4, numbers 1-5. The distal articular

surface is lateromedialy expanded in sauropods and presents a deep intercondylar surface (McIntosh 1990; pers. obs.). The femora distal articular surface is flat, perpendicular to the major axis, in less derived sauropods, and becomes increasingly laterally angled in titanosaurs (Wilson and Sereno 1998; Wilson and Carrano 2005) - figure 5.4. One could also observe that both anterior and posterior intercondylar groves are deeper in sauropods than in prosauropods, which originates that sauropods exhibit a narrow anteroposterior central distal articular surface.

In some sauropods a lateral depression could be observed, on the distal articular surface (e.g., *Apatosaurus*, fig. 5.4, number 8). This morphology, together with a rugose surface, seems to indicate the existence of a large amount of cartilaginous material in this area.

Concerning the proximal articular surface, it has been said that the posterior *sulcus* "migrates" laterally in sauropods, which reveal an increase of the anteroposterior length of the proximal articular surface.

The characteristic posterior projection of prosauropods is therefore strongly reduced in derived sauropodomorphs, in which it becomes flatter, while neosauropods display a posterior curved contour. The light anterior curving of the proximal articular surface of prosauropods turns into a straighter or concave anterior contour in sauropods – figure 5.5.

The existence of two types of sauropod stances – wide- and narrow-gauge – has been traditionally identified on the ichnological record (Farlow et al. 1989; Farlow 1992; Lockley, Farlow, and Meyer 1994; Moratalla et al. 1994a).

The two ichnotypes reflect two groups of distinct stances of sauropod dinosaurs: derived sauropods, like titanosaurs, produced wide-gauge trackways (*manus* and *pes* prints are well apart from the midline) and less derived sauropods produced narrow-gauge trackways (both *manus* and *pes* prints approach or intersect the trackway midline).

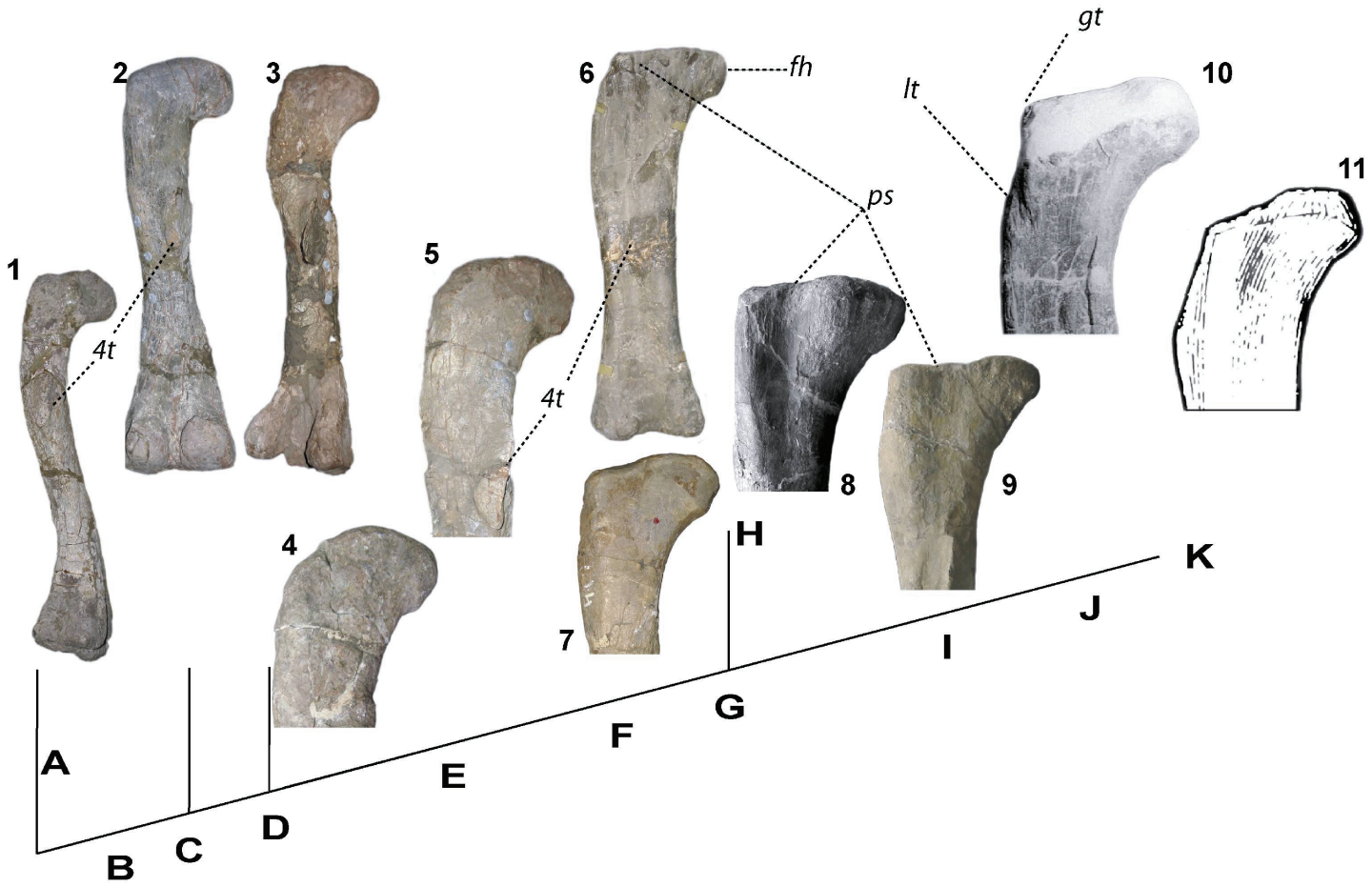

Figure 5.2 Sauropodomorpha left femora posterior view (except 5 in anterior view). 1) *Herrerasaurus ischigualastensis* (PVL 2566; reversed); 2) *Coloradisaurus brevis* (PVL 5904; reversed); 3) *Riojasaurus incertus* (PVL 3663); 4) *Gyposaurus sinensis* (IVPP V26); 5) *Lessemsaurus sauropoides* (PVL 4822 -65; reversed); 6) *Mamenchisaurus guangyuanensis* (CDUTM O21; reversed); 7) *Volkheimeria chubutensis* (PVL 4077); 8) *Diplodocus longus* (CM 21754; reversed); 9) *Camarasaurus lentus* (CM 21772); 10) *Epachthosaurus sciuttoi* (adapted from Martinez et al. 2004; reversed); 11) *Saltasaurus loricatus* (adapted from Powell 1980, Fig. 37a). Abbreviations: A – Theropoda; B – Sauropodomorpha; C – Plateosauria; D – Sauropodiformes; E – Sauropoda; F – Eusauropoda; G – Neosauropoda; H – Diplodocoidea; I – Macronaria; J – Titanosauria; K – Lithostrotia. Abbreviations – 4t – fourth trochanter; fh – femoral head; gt – greater trochanter; lt – lateral trochanter; ps – posterior sulcus. Bones are normalized approximately to the same length for comparison.

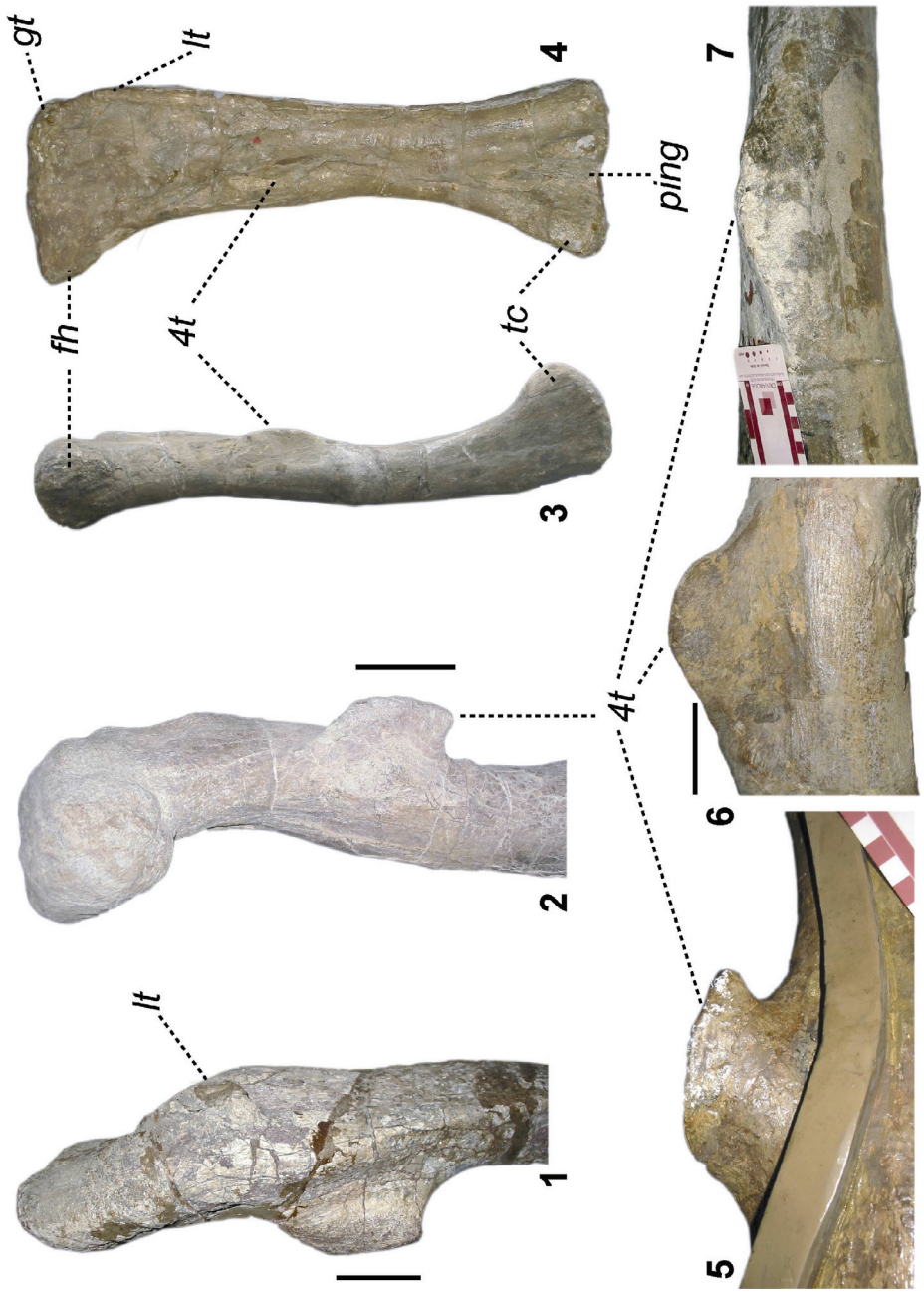

Figure 5.3 Femora of different sauropodomorphs – Fourth Trochanter relative position and shape: 1) - *Herrerasaurus ischigualastensis* (PVL 2566) right femur, lateral view. scale bar – 5 cm; 2) - *Yunnanosaurus youngi* (LDM non-numbered) right femur, posteromedial view. scale bar – 10 cm; 3) - *Camarasaurus* (?)*lentus* (CM 21772) right femur, medial view. femur length – 56 cm; 4) - *Bellusaurus sui* (IVPP 83003) right femur, posterior view. femur length – 140 cm; 5) - *Lufengosaurus huenei* (IVPP V.15) left femur, lateral view of 4th trochanter. scale – each square 1 cm; 6) - *Patagosaurus fariasi* (MACN CH 934) right femur, medial view of 4th trochanter. scale bar – 4 cm; 7) - *Barosaurus africanus* (MB 2700), right femur, medial view of 4th trochanter. scale – each square 1 cm. Abbreviations: 4t – Fourth Trochanter; fh – femoral head; gt – greater trochanter; lt – lateral trochanter; ping – posterior intercondylar groove; tc – tibial condyle .

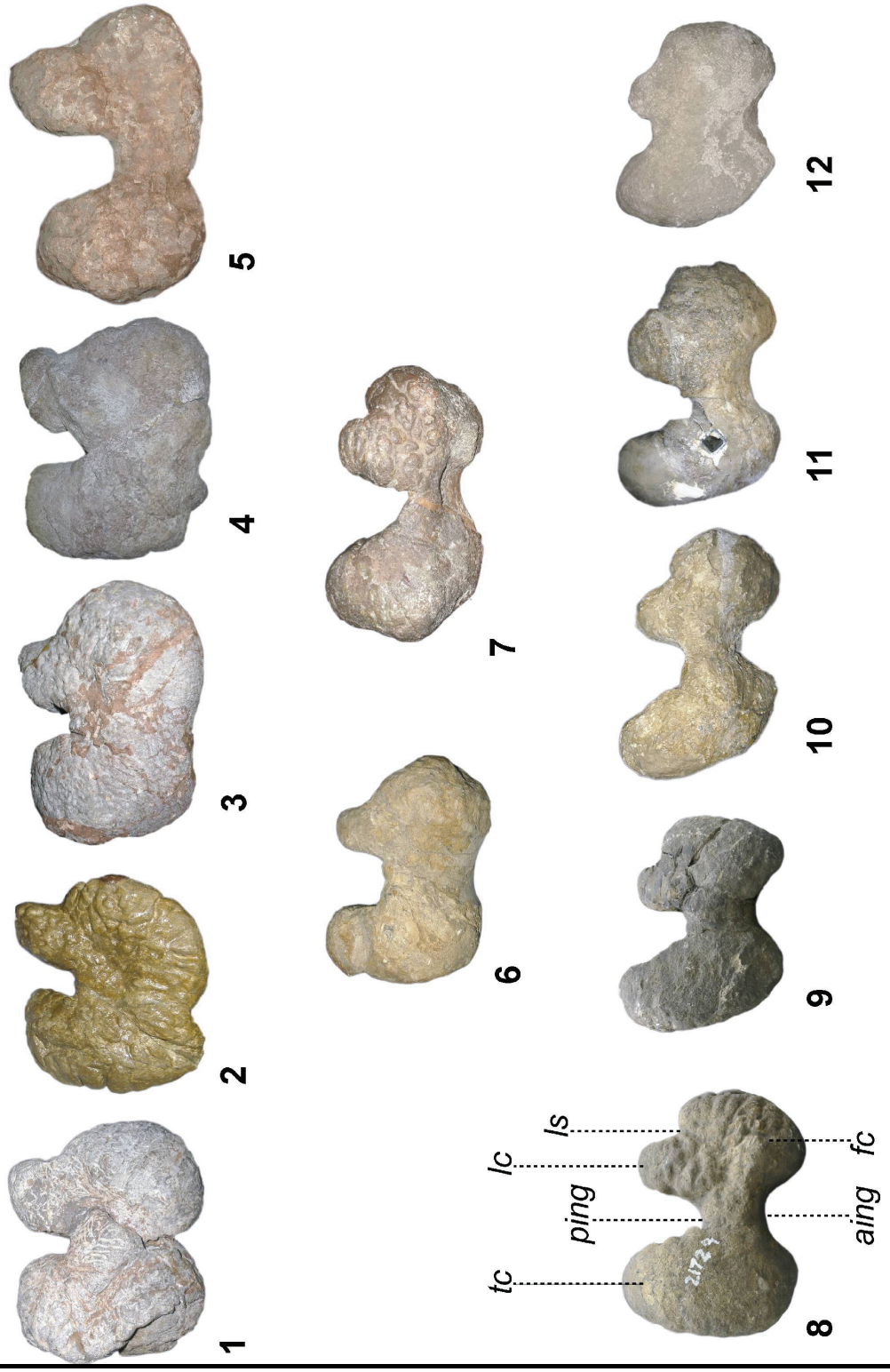

Figure 5.4 Distal articular surface view of right femora of different sauropodomorphs 1 - *Lufengosaurus sp.* (LDM 0604; reversed); 2 - *Plateosaurus engelhardti* (MD indivi. VI); 3 - *Coloradisaurus brevis* (PVL 5904); 4 - *Yunnanosaurus youngi* (LDM non-numbered); 5 - *Lessemsaurus sauropoides* (PVL 4822/65); 6 - *Patagosaurus fariasi* (MACN CH 934); 7 - *Mamenchisaurus sp.* (IVPP exhibition specimen; reversed); 8 - *Apatosaurus louisae* (CM 21729); 9 - *Diplodocus longus* (CM 21754; reversed); 10 - *Bellusaurus sui* (IVPP 83003); 11 - *Brachiosaurus brancai* (MB SII); 12 - *Gobititan shenzhouensis* (IVPP 12579; reversed). Abbreviations: aing – anterior intercondylar groove; fc – fibular condyle; lc – lateral condyle; ls – lateral sulcus; ping – posterior intercondylar groove; tc – tibial condyle. Bones are normalized approximately to the same length for comparison.

Wilson and Carrano (1999) interpreted those differences on the basis of distinct femoral morphologies in the two sub-groups of sauropods, namely “outwardly angled femoral posture and beveled knee condyles, along with a more asymmetrical femoral midshaft” (p. 265).

The femoral morphological differences pointed by Wilson and Carrano (1999) as the principal biomechanical basis of narrow- and wide-gauge locomotion in sauropods were complemented afterwards. Henderson (2006) referred the relative positions of those animals centers of mass, namely that narrow-gauge walking was the primitive trait for sauropods, and that this gait was a requirement for large (>12.5 tons.) sauropods (e.g., *Brachiosaurus* possess more anteriorly positioned center of mass) (*idem, ibidem* p. 920). Henderson (2006) even stated that this pattern arose independently within different clades of sauropods.

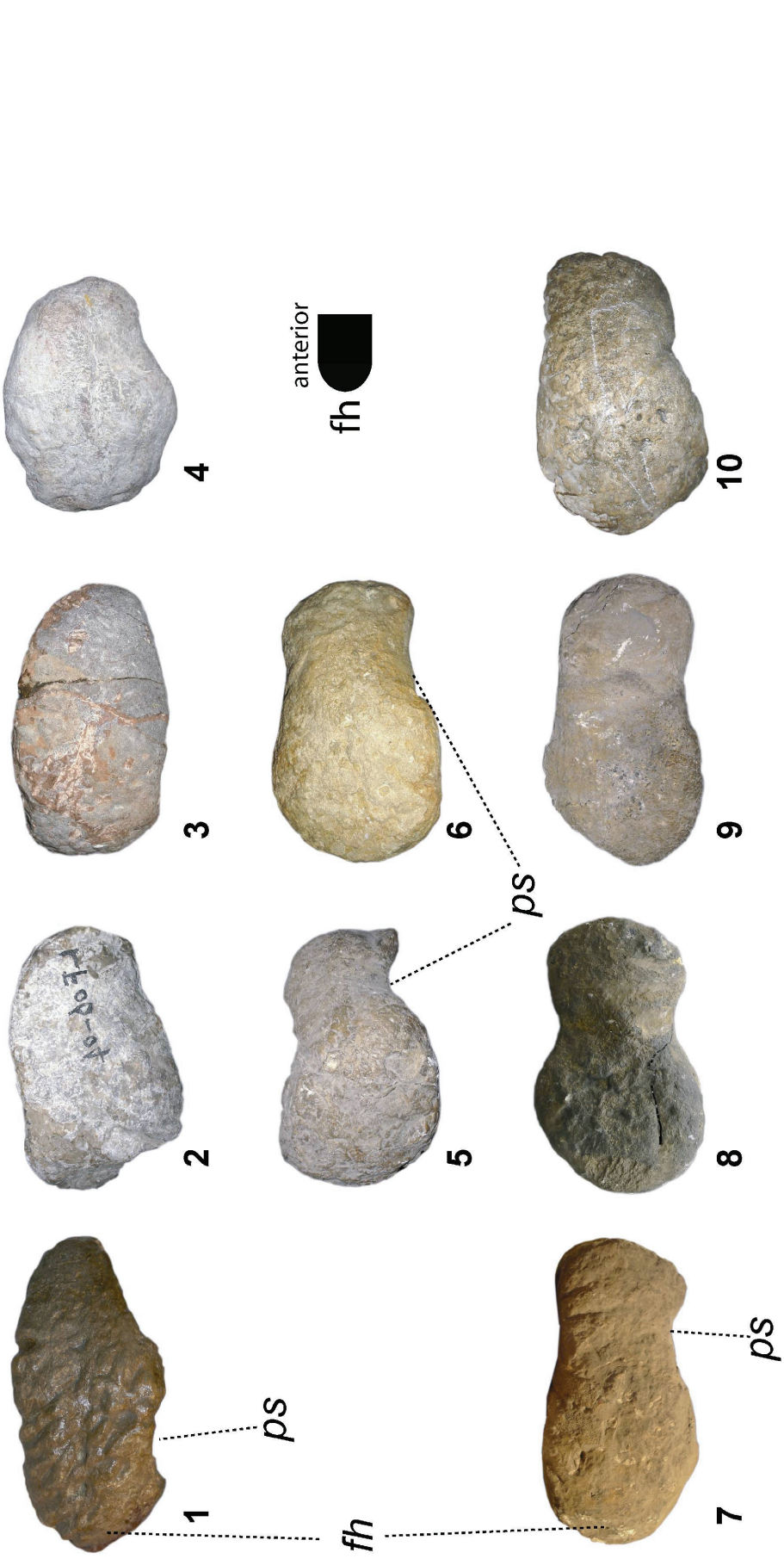

Figure 5.5 Proximal articular surface view of right femora of different sauropodomorphs 1 - *Plateosaurus engelhardti* (MD indivi. VI; reversed); 2 - *Lufengosaurus sp.* (LDM 0604; reversed); 3 - *Coloradisaurus brevis* (PVL 5904); 4 - *Yunnanosaurus youngi* (LDM non-numbered); 5 - *Patagosaurus fariasi* (MACN Pv CH 1986; reversed); 6 - *Volkheimeria chubutensis* (PVL 4077; reversed); 7 - *Barosaurus africanus* (MB 2637); 8 - *Diplodocus longus* (CM 21754; reversed); 9 - *Camarasaurus* (?)*lentus* (CM 21772); 10 - *Brachiosaurus brancai* (MB SII). Abbreviations: fh – femoral head; ps – posterior sulcus. Bones are normalized approximately to the same length for comparison.

Humerus

The humerus of sauropodomorphs is an expanded bone, both proximal and distally. The relative size and shape of this element differs considerably among sauropodomorphs, although it is generally smaller than the femur, except in Brachiosaurus. The deltopectoral crest is one of the easiest recognizable morphologies in the anterolateral surface, extending from the proximal anterior shaft to a half length, depending on the groups. This area of muscular insertion is well developed in Prosauropods and, in some cases, presents an almost planar surface - e.g., figure 5.7, numbers 1-3.

The deltopectoral crest is low but pronounced in sauropods, the exception for that condition being the brachiosaurids, in which it is well developed, displayed in elongated humeri, sub-equal in length to femora (Wilson and Sereno 1998). Despite constituting a character in sauropod phylogenies (*idem, ibidem*), it has never been previously quantified in terms of development or relative positioning.

Unlike prosauropods, the humerus proximal articular surface of sauropods is lateromedially *quasi* symmetric and presents an anteroposteriorly expansion that varies among clades. Non-sauropod sauropodomorphs show an asymmetrical proximal third which is more medially expanded, the medial surface forming a well pronounced arch - figure 5.6, numbers 1-2 and figure 5.7, number 1).

The distal end exhibits anteriorly, in some species, two morphological structures that vary from small and very close bumps to well developed and well separated, the latter herein designated lateral and medial ridges - figure 5.6, numbers 4-5 and figure 5.7, number 7). These structures have been interpreted as probable muscle insertions (Schwarz et al. 2007). Based on histological analysis of sauropods preserved cartilage, the humeral distal articular surface has been reconstructed and it was inferred that most of this surface was covered by cartilage, being the lateral and

medial ridges the probable insertions of the *m. brachialis inferior* (Schwarz et al. 2007, fig. 5).

In prosauropods the distal articular surface is not totally flat and perpendicular to the humerus main axis, being longer medially - e.g., figure 5.6, numbers 1-2 and figure 5.7, number 1. This morphology could have constrained the extension amplitude of the forelimb of those 'prosauropods'. Laterally in the distal articular surface a flat surface could be noted which is not observed in sauropods - figure 5.7, number 6.

The proximal articular surface anteroposterior length varies among sauropodomorphs, the discrepancies observed depending mainly on the extent of the posterior projection. *Riojasaurus incertus* (PVL 3808) displays a big humeral head, deflected posterodistally, which contributes to increase the anteroposterior extent of the proximal articular surface of the humerus. Similar morphology could be observed in prosauropods as, for example, *Coloradisaurus brevis* (PVL 5904), *Lufengosaurus huenei* (IVPP V15) or *Massospondylus carinatus* (BMNH R.8181). Some sauropods also display a big posterior expansion of the humeral head, such as *Barosaurus africanus* (MB 2656) or *Patagosaurus fariasi* (MACN 932 – fig. 5.7, number 5). *Brachiosaurus brancai* (MB SII) proximal articular surface is asymmetric and with a massive medial half, exhibiting a posterior projection located more distally than the proximal articular surface. *Shunosaurus lii* (ZDM 5008) exhibits, laterally to the posterior projection of the humeral head, a rounded bump, possibly the insertion of *supracoracoideus* process (pers. obs. 2006).

Prosauropods proximal asymmetry results from the straightness of the medial side (figs. 5.6 1-2 and 5.7 1), contrary to what is observed in sauropods, in which the proximal surface is rounded, only varying in its lateromedial extent.

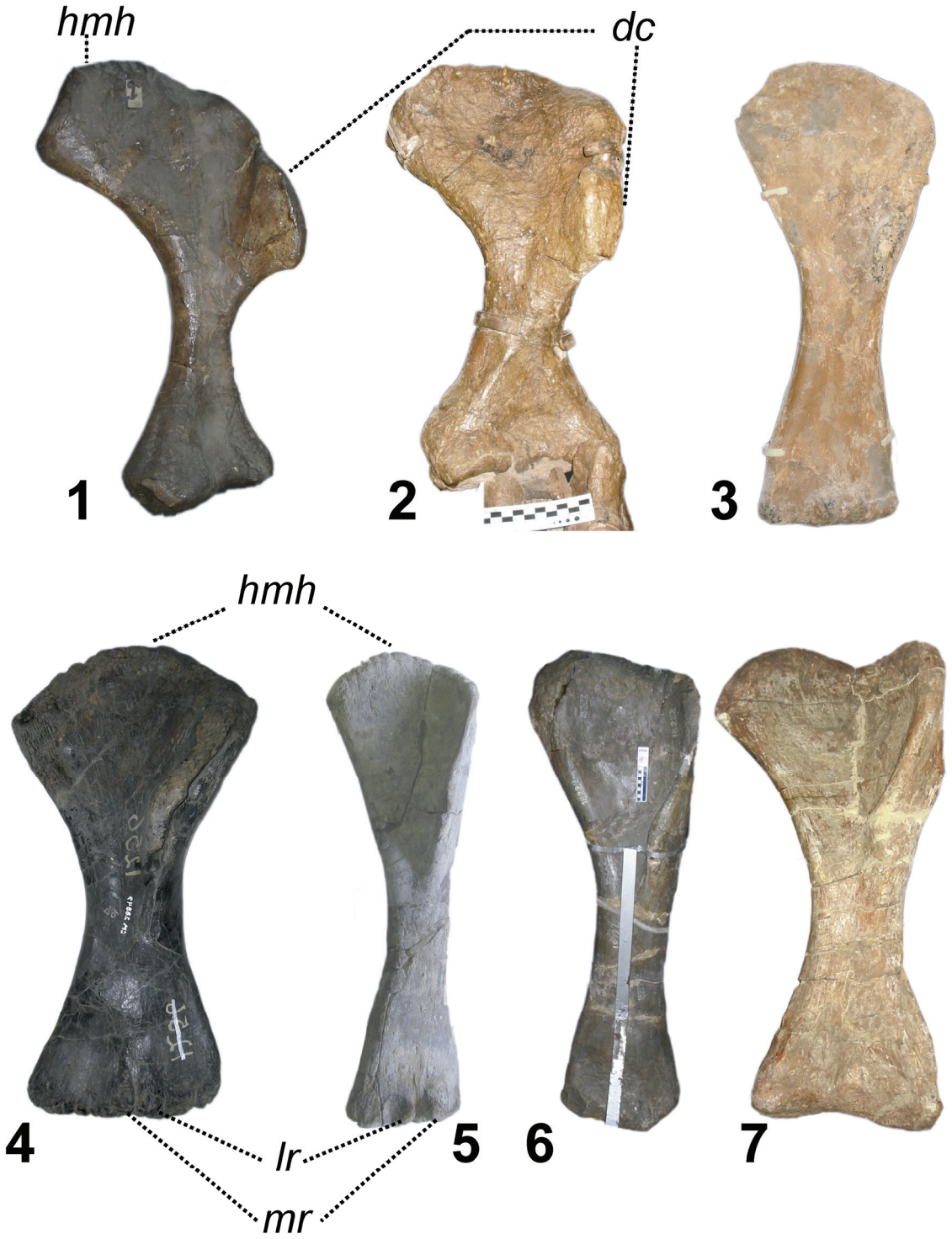

Figure 5.6 Left humeri of distinct sauropodomorphs, in anterior view 1 - *Lufengosaurus huenei* (IVPP V.15; reversed); 2 - *Jingshanosaurus xinwaensis* (LFM LFM 003.1; exhibits partly proximal zeugopodium); 3 - *Shunosaurus lii* (ZDM 5008); 4 - *Apatosaurus sp.* (CM 28849; reversed); 5 - *Bothriospondylus madagascariensis* (MHNM MAA 164); 6 - *Chubutisaurus insignis* (MACN PV 18222); 7 - *Saltasaurus loricatus* (PVL 67). Abbreviations: dc – deltopectoral crest; hmh – humeral head; lr – lateral ridge; mr – medial ridge. Bones are normalized approximately to the same length for comparison.

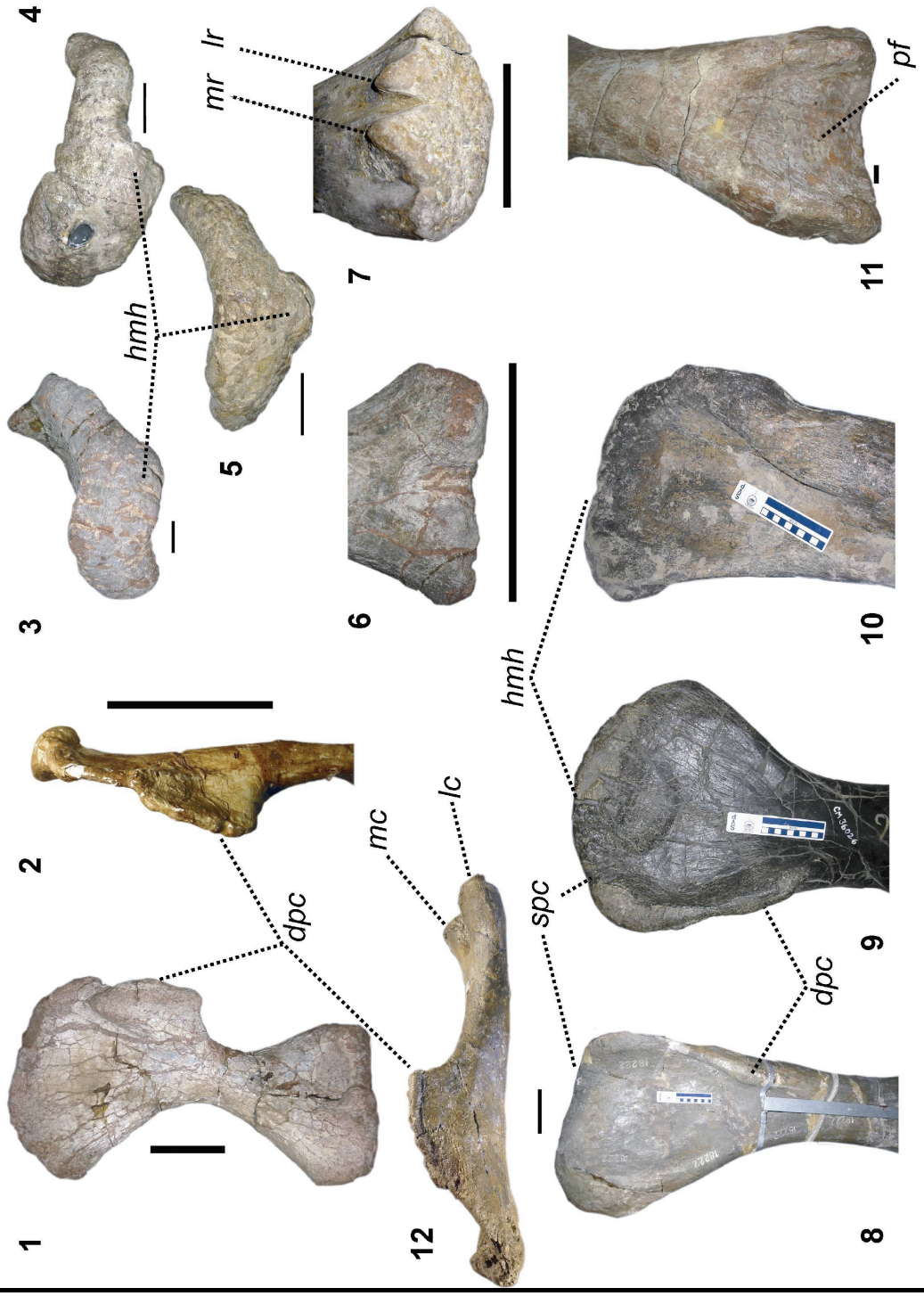

Figure 5.7 Sauropodomorphs humeri morphological aspects. 1 - *Riojasaurus incertus* (PVL 3808) left humerus, anterior view; 2 - *Massospondylus carinatus* (BMNH R8171; reversed) left humerus, lateral view; 3 - *Coloradisaurus brevis* (PVL 5904) right humerus, proximal view of the proximal articular surface; 4 - *Brachiosaurus brancai* (MB SII), right humerus, proximal view of the proximal articular surface; 5 - *Patagosaurus fariasi* (MACN CH 932) right humerus, proximal view of the proximal articular surface; 6 - *Coloradisaurus brevis* (PVL 5904) right humerus, anterior view of distal third; (7) *Bothriospondylus madagascariensis* (MHNM MAA 164) right humerus, oblique view of distal surface; 8 - *Chubutisaurus insignis* (MACN PV 18222) left humerus, anterior view; 9 - *Apatosaurus sp.* (CM 28849) right humerus, anterior view; 10 - *Aelosaurus sp.* (CPLB cast of Museo Provincial de Cipolletti, Rio Negro MPCA 2710) left humerus, anterior view; 11 - *Chubutisaurus insignis* (MACN PV 18222) right humerus, posterior view of the distal third; 12 - *Plateosaurus engelhardti* (MD N13) right humerus, lateral view. Abbreviations: dc – deltopectoral crest; hmh – humeral head; lc – lateral condyle; lr – lateral ridge; mc – medial condyle; mr – medial ridge; pf – posterior fossa; spc – supracoracoideus process (probable area of insertion). Scale bars: 10 cm in 1-2, 4, 6, 7-10; 2 cm in 3 and 11-12; 5 cm in 5.

5.2.2 Zeugopodium (paired segment of the tetrapod limb corresponding to the fore limb -radius and ulna, and hind limb - tibia and fibula)

Tibia

Prosauropods tibiae are morphological very similar to theropods, namely by being more slender than in sauropods (figure 4.8). Sauropod tibiae are, similarly to other appendicular elements, robust and massive structures, constituting the zeugopodial element that supports most of the weight. The fibula importance concerning the weight bearing remains mainly in providing areas of muscular attachment.

Laterally in the tibia an area of muscular attachment designated cnemial crest could be noticed - figure 5.8. The cnemial crest is the area where the thigh muscles are attached. It is functionally linked to power transmission of the quadriceps tendon to the tibia and, in sauropods, is a developed area, anteriorly directed, in which the proximal end of the fibula is articulated (Wilson and Sereno 1998) - figure 5.8, numbers 5, 6 and 10.

Sauropods reveal a reduction in the tibial cnemial crest along its evolutionary history, which seems to be associated with a reduction in the use of the lower limb (Carrano 2005), since it is the insertion area of the knee extensor muscles (Romer 1956). This fact is justified by the morphological changes associated with a more supporting skeleton and graviportal pose of sauropods. Prosauropods, instead, reveal a relatively developed cnemial crest which implies a higher use of the zeugopodium in the locomotion.

The distal articular surface of the sauropod tibia shows a U shape, in distal view, and is clearly distinguished by two main morphological features, similar to condyles – the posteroventral process and the distal ascending process, which receives the astragalar ascending process, which is lateral - figure 5.8, numbers 7-9.

The ascending process articulates with a comparable process of the astragalus. The posteroventral process in sauropods does not extend laterally, as in prosauropods, originating an exposure of the posterior *fossa* of the astragalus (Wilson and Sereno 1998; pers. obs.).

Radius

The radius of sauropodomorphs is a slightly arched bone, although in sauropods the curvature is reduced and in *Apatosaurus* it is almost straight (Wilson and Sereno 1998). The proximal articular surface of sauropods radii is ovate in shape, and the posteroproximal border articulates into the anterior *fossa* of the ulna. In prosauropods the proximal articular surface is oval shaped and thicker laterally than medially.

The radius is usually more expanded distally than proximally, revealing a light projection which is the ulnar articular process. The relative orientation of radius and ulna induced a considerable amount of functional debates. Wilson and Sereno (1998) considered that sauropods proximal radius was anterior and lateral to the ulna as in other saurischians, while the ulna distal portion lies anteriorly to the radius, implying a partial crossover. Other authors suggested that the radius is placed medially with a parallel position of the radius and ulna (Bonnan 2003). This placement of the fore limb zeugopodium permitted "…that both bones were more or less parallel to one another might have augmented the forelimb of sauropods to reduce shear stress during the support phase." (Bonnan 2003, p. 609).

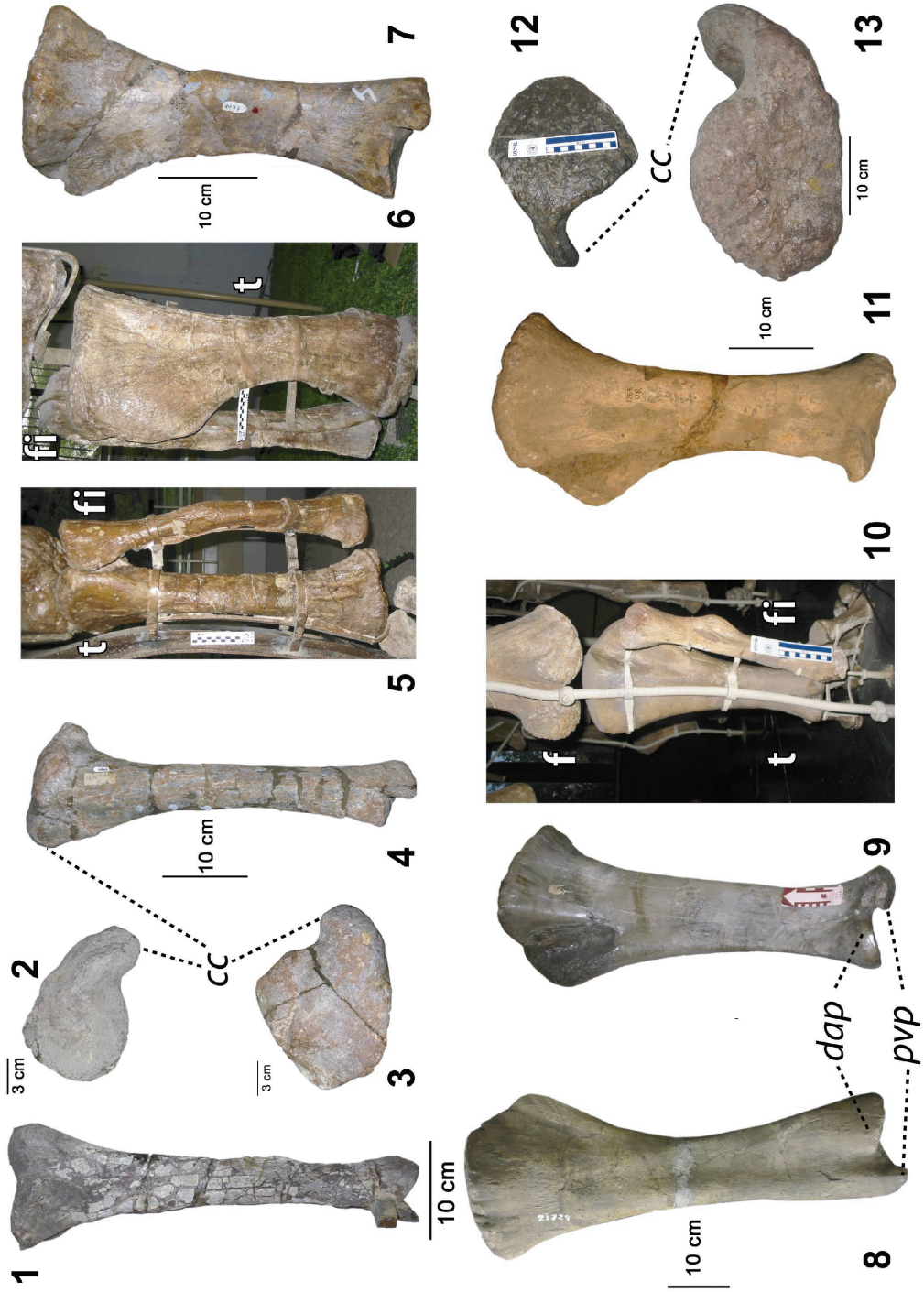

Figure 5.8 Tibiae of diverse Saurischia: 1 - *Herrerasaurus ischigualastensis* (PVL 2566) right tibia in posterolateral view (PVL 2566) and 2 proximal articular surface; 3 - *Coloradisaurus brevis* (PVL 5904) left tibia in posterior view and 4 - proximal articular surface; 5 - *Jingshanosaurus xinwaensis* (LFM 003.1) left tibia and fibula in anterior view - scale bar = 13 cm; 6 - *Mamenchisaurus guangyuanensis* (CDUTM O21) right tibia in anteromedial view - scale bar = 13 cm; 7 - *Saltasaurus loricatus* (MLP CS1264) left tibia in posterolateral view; 8 - *Apatosaurus louisae* (CM 21729) right tibia in posterolateral view; 9 - *Brachiosaurus brancai* (MB SII) left tibia in posterolateral view - scale bar = 16.5 cm; 10 - *Neuquensaurus australis* (MLP CS1093) right tibia and fibula in posterolateral view - scale bar = 15.8 cm; 11 - *Volkheimeria chubutensis* (PVL 4077) right tibia in posterolateral view; 12 - *Apatosaurus excelsus* (CM 556) left tibia proximal articular surface - scale bar = 15.8 cm; 13 - *Titanosauria* indet. (MCF-PVPH 103) proximal articular surface. Abbreviations: cc - cnemial crest; dap - distal ascending process; f - femur; fi - fibula; pvp - posteroventral process; t - tibia.

Ulna

Most of the sauropods present zeugopodium muscle attachments both in fore and hind limb. One of those areas is the ulnar olecranon process, located in the proximal articular surface, which in sauropods is triradiate. That process is usually a round projection in theropods and prosauropods, while flat and rugose in less derived sauropods (Wilson and Sereno 1998). This condition has been observed, for example, in the prosauropod *Jingshanosaurus xinwaensis* (pers. obs. 2006; LFM 003.1), which has a curved olecranon process with its peak between ulnar processes – figure 5.9, number 12.

The superior development of the ulnar process is characteristic of derived sauropods like titanosaurians; this could be defined as a reacquisition of the olecranon process (Christiansen 1997; Wilson and Sereno 1998; Powell 2003). The underdevelopment in non-titanosaurian sauropods facilitates the columnar posture of the limbs and is associated with similar morphological changes linked with a reduction of lower limb flexor attachment sites, for example, the cited cnemial crest (Carrano 2005). In titanosaurians, the full extension of the forelimb is achieved by the existence of a *fossa* in the posterior face of the humerus (Wilson and Sereno 1998; Bonnan 2003) - see *Chubutisaurus insignis* (MACN PV 18222), figure 5.7, number 11.

5.2.3 Autopodium (the most distal portion of the tetrapod limb, including the carpals and tarsals, metapodials, and phalanges)

Manus

Prosauropods possess *manus* with grasping ability, a consequence of the strongly twisted and mobile pollex (Galton 1971; Galton 1990). *Plateosaurus* was considered as a non-typical biped because it presented a developed thumb with a large and trenchant claw (e.g. Van Heerden 1997).

In non-eusauropod sauropods, one of its most basal forms – *Antetonitrus*, exhibits a grasping manus, more characteristic of bipedal forms (Barrett and Upchurch 2007), despite the fact that its limb proportions suggest a quadrupedal locomotion (Wilson 2002). More derived forms, as *Vulcanodon*, present more weight-bearing *manus* (Cooper 1984; Barrett and Upchurch 2007), typical of the sauropod autopodial condition.

The increase in body mass has morphological consequences in the appendicular skeleton, as seen, and particularly in the autopodium of sauropodomorphs. Some of these trends consist in a more columnar and bounded metacarpus, subunguligrade pes, and a gradually reduction in both number and size of autopodial phalanges (Wilson and Sereno 1998).

The evolution of U-shaped *manus* in sauropods (McIntosh 1990; Upchurch 1995, 1998; Wilson and Sereno 1998) increases the mechanical resistance required for a graviportal stance. Sauropod metacarpals, therefore, acquired a semicircular, columnar arrangement, with reduction in length disparities between elements and with a subtriangular proximal end. This proximal morphology allows that metacarpals interlock forming an arch of 270º (Wilson and Sereno 1998) - figure 5.10, numbers 5-6.

Other authors suggested that this characteristic *manus* in not due to mass increase, but to differences in positioning of the radius relatively to the ulna, being this fact the driving pressure for the referred arrangement of some sauropods *autopodium* (e.g., Bonnan 2003).

Diplodocoids reveal short and heterogeneous metacarpals (Gilmore 1936) and sauropod *manus* exhibit a phalangeal reduction along its clade, which is accomplished to the point that all unguals and most of the phalanges are eventually lost. This reduction/loss of bone elements in sauropod *manus* implicates a reduction/loss of flexion and extension in the fore limb autopodium.

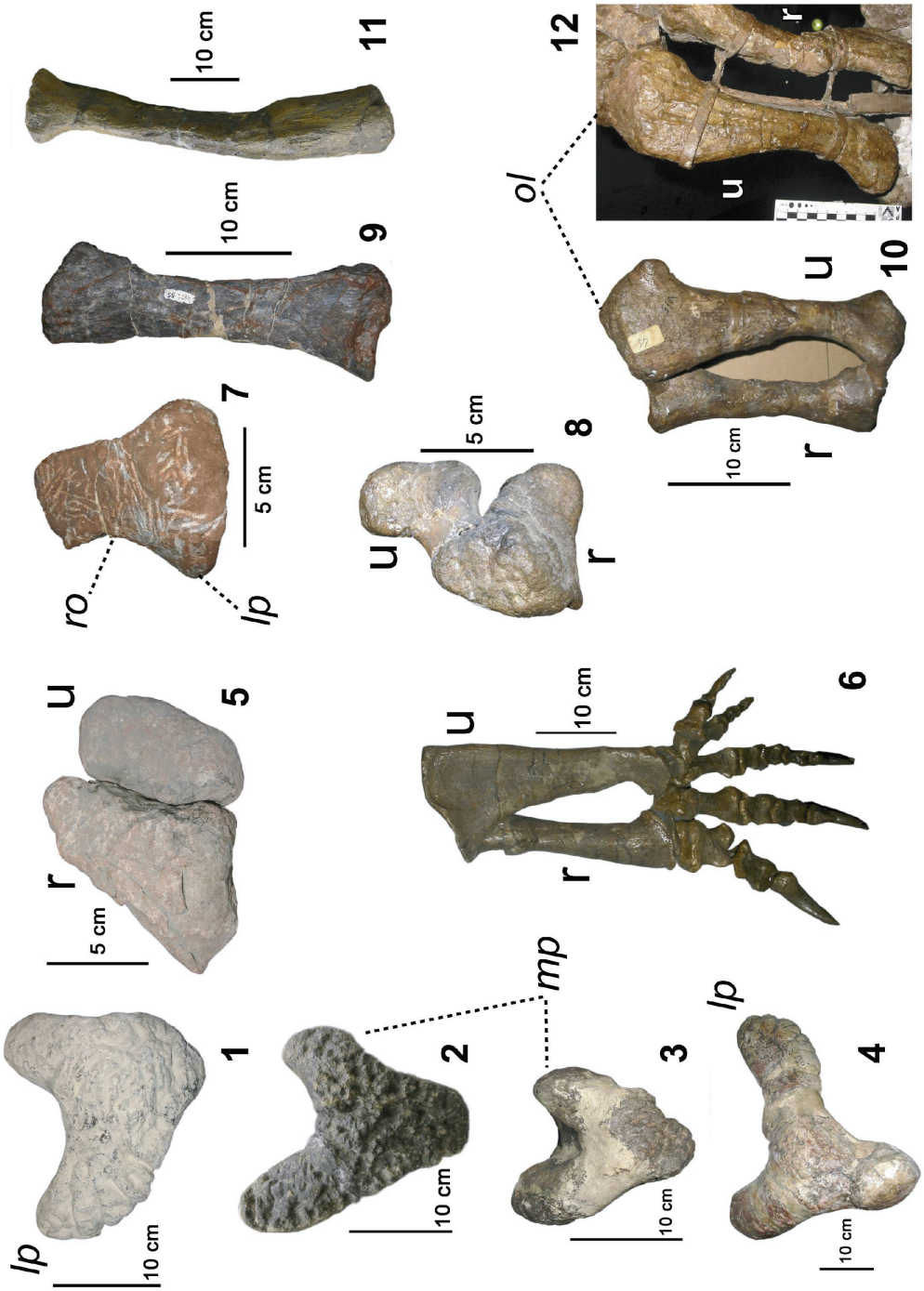

Figure 5.9 Radius and ulna of diverse sauropodomorphs: 1 - *Tornieria africana* (MB.R.2586) right ulna in proximal view; 2 - *Apatosaurus excelsus* (CM 555) right ulna in proximal view; 3 - *Amargasaurus cazaui* (MACN PVN15) right ulna in proximal view; 4 - *Brachiosaurus brancai* (MB SII) left ulna in proximal view; 5 - *Riojasaurus incertus* (PVL 3808) right ulna and radius in proximal view; 6 - *Plateosaurus engelhardti* (MD indivi. VI) right ulna, radius and manus. Radius and ulna in medial view and manus in ventral view; 7 - *Lessemsaurus sauropoides* (PVL 4822/54) left ulna in proximal view; 8 - *Lufengosaurus huenei* (IVPP V.040) right radius and ulna in proximal view - note that radius and ulna are connected with preparation material; 9 - *Lessemsaurus sauropoides* (PVL 4822/55) left radius in medial view; 10 - *Lufengosaurus huenei* (IVPP V.040) right radius and ulna in posterolateral view; 11 - *Apatosaurus louisae* (CM 30766) right radius in medial view; 12 - *Jingshanosaurus xinwaensis* left ulna in posteromedial view (LFM 003). Abbreviations: lp - lateral process; mp - medial process; ol - olecranon; r - radius; ro - radial fossa; u - ulna.

Therefore, along the sauropodomorph evolutionary history, there seems to be a transformation from a propulsive and digitigrade *manus* to an autopodial columnar structure able to support big weights (Carrano 1998, 2000; Wilson and Sereno 1998; Wilson 2002; Bonnan 2003).

Recent biomechanical analysis of fore limbs of *Plateosaurus* and *Massospondylus* indicated that these sauropodomorphs were unable of active quadrupedal locomotion (Bonnan and Senter 2007). This conclusion came fundamentally from the incapability of *manus* pronation in those species.

The capacity of pronation and supination of the *manus* is linked with the development of semi-tubular *manus* and a quadrupedal stance in sauropods and has been formerly established by other authors (Bonnan 2003), who stated that all those morphological changes form a complex functional suite.

Thus, the appearing of quadrupedality in sauropodomorphs more derived than *Melanorosaurus* is associated with an increase in body size and changes in *manus* structure (Carrano 2005). These two factors are usually associated with quadrupedal locomotion due to a reduction in mobility in the *carpus* - through fusion and/or loss of elements (*idem*, *ibidem*).

The analysis of an almost complete series of *Massospondylus carinatus* fore limb as well as axial and cranial elements permitted allometric inferences, namely the ontogenetic change of the locomotion – juvenile's obligate quadrupedality gave rise to mature facultative bipedality (Reisz et al. 2005). These authors even suggest some phylogenetic implications for locomotion, relating the acquisition of quadrupedality in sauropods with the retardation of post-natal negative allometry of the forelimbs, that is to say, appendicular heterochrony (Reisz et al. 2005). This study also carries behavioral implications, since juveniles are classified as altricial based on the limb proportions as well as the limited efficient quadrupedal locomotion (Reisz et al. 2005; Bonnan and Senter 2007).

The phylogenetic closeness of *Massoposndylus* and *Plateosaurus* allow the suggestion that a similar developmental trajectory was probably present in the former taxon as well (Bonnan and Senter 2007).

Histological analysis of *Plateosaurus* and *Thecodontosaurus* reveals that growth was cyclical but rapid until sexual maturity was reached. Later on, the growth rate is reduced but is still greater than reptilian rates (Sander et al. 2004).

Pes

Prosauropods have five metatarsals (Galton and Upchurch 2004), being metatarsal III the longest, the size reducing both laterally and medially, which gives the hind limb autopodium a symmetrical shape, i.e., revealing a mesaxonic structure - figure 4.10, numbers 1 and 3-5. The ichnological record has confirmed that prosauropods *pes* are functional tetradactyl due mainly to the extreme reduction of digit V (Thulborn 1990), also presenting a medial rotation of the digits.

Sauropods, in turn, reveal an asymmetrical *pes* - entaxonic structure - due mainly to the robust medial digits (I-III), being the lateral ones more gracile. This trend is more evident in neosauropods than in more primitive sauropods like *Omeisaurus* - compare figure 5.10, numbers 6 and 8.

The metatarsals distinct lengths and morphologies imply a bigger weight support on the *pes* medial margin than on the lateral side. The stated asymmetrical weight-bearing of sauropod *pes* is corroborated by the deep lateral margins observed in a considerable number of sauropod tracks (e.g., Farlow et al. 1989; Santos et al. 1994).

The inferred mobility of sauropod *pes* is bigger when compared to other graviportal dinosaurs or mammals (Bonnan 2001), namely through the movement of digits I-III, that would have rolled back in flexion, “helping to drive the claws further into the substrate and giving the large pes crampon-like traction against the substrate.”

(*idem*, *ibidem*, p. 471). The digit rotation has been identified as the main factor of shape variability in sauropodomorphs *pes* tracks (Rodrigues and Santos 2004).

Wilson and Sereno (1998) pointed out that sauropods developed a semi-plantigrade posture of *pes* due mainly to a reorientation of the astragalus. In Eusauropoda, the pedal unguals are not symmetric, exhibiting anterollaterally beveled articular surfaces. This morphology seems to indicate that “the claws were deflected laterally relative to digit III axis” (Wilson and Carrano 1999, p. 258) - figure 5.11, number 8.

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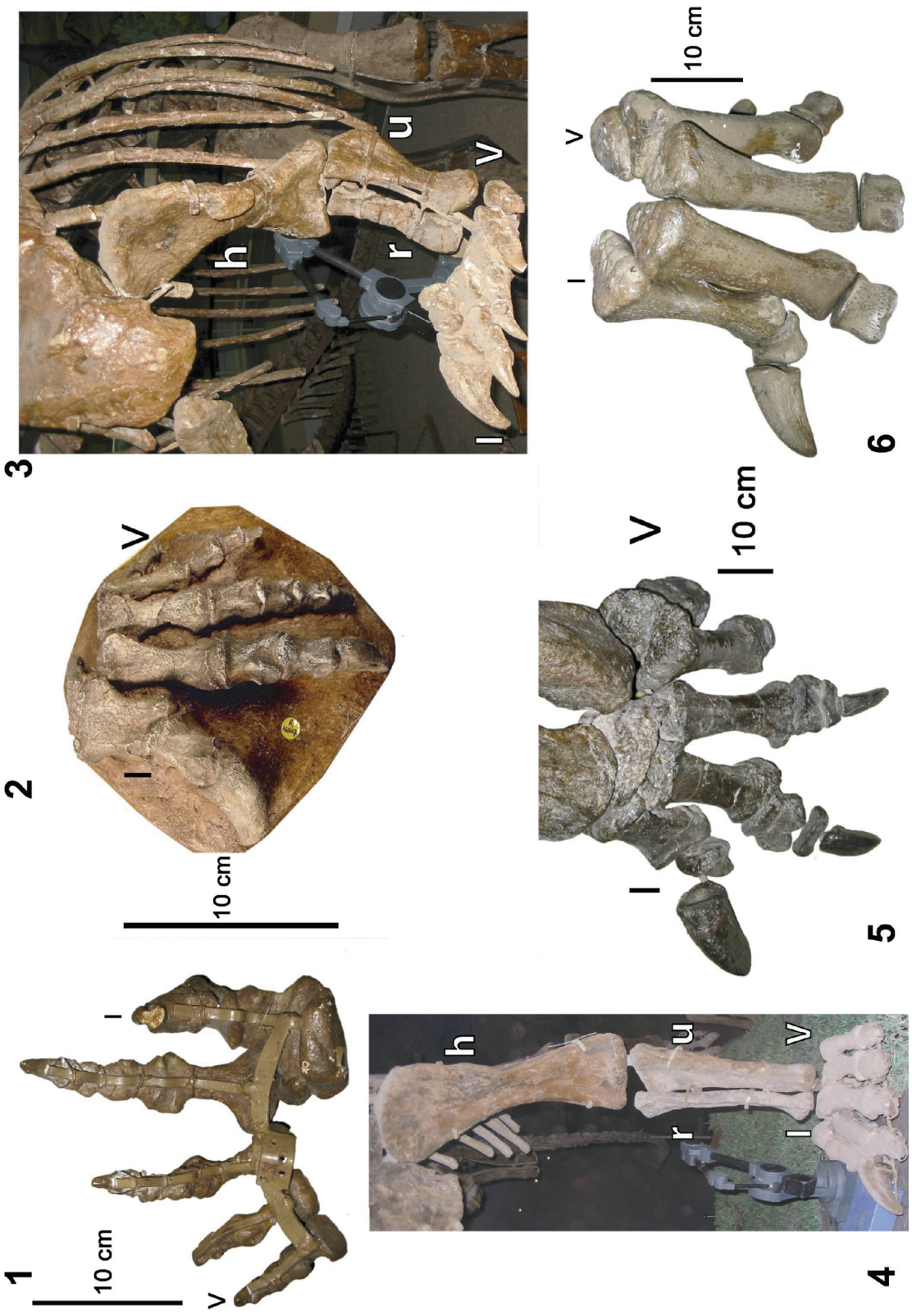

Figure 5.10 Manus of sauropodomorphs: 1 - *Lufengosaurus huenei* (IVPP V.040) right manus in ventral view; 2 - *Massopondylus carinatus* (BMNH 16507) cast of right manus in dorsal view; 3 - *Jingshanosaurus xinwaensis* (LFM LFM 003.1) left manus in anterolateral view - exhibits zeugopodium and stylopodium; 4 - *Shunosaurus lii* (ZDM 5008) left manus in anterolateral view - exhibits zeugopodium and stylopodium; 5 - *Apatosaurus lousiae* (CM 3018) left manus in anterodorsal view; 6 - *Dicraeosaurus hansemanni* (MB mounted skeleton) left manus in anterodorsal view. Abbreviations: I - metatarsal/digit I; V - metatarsal/digit V; h - humerus; r - radius; u - ulna.

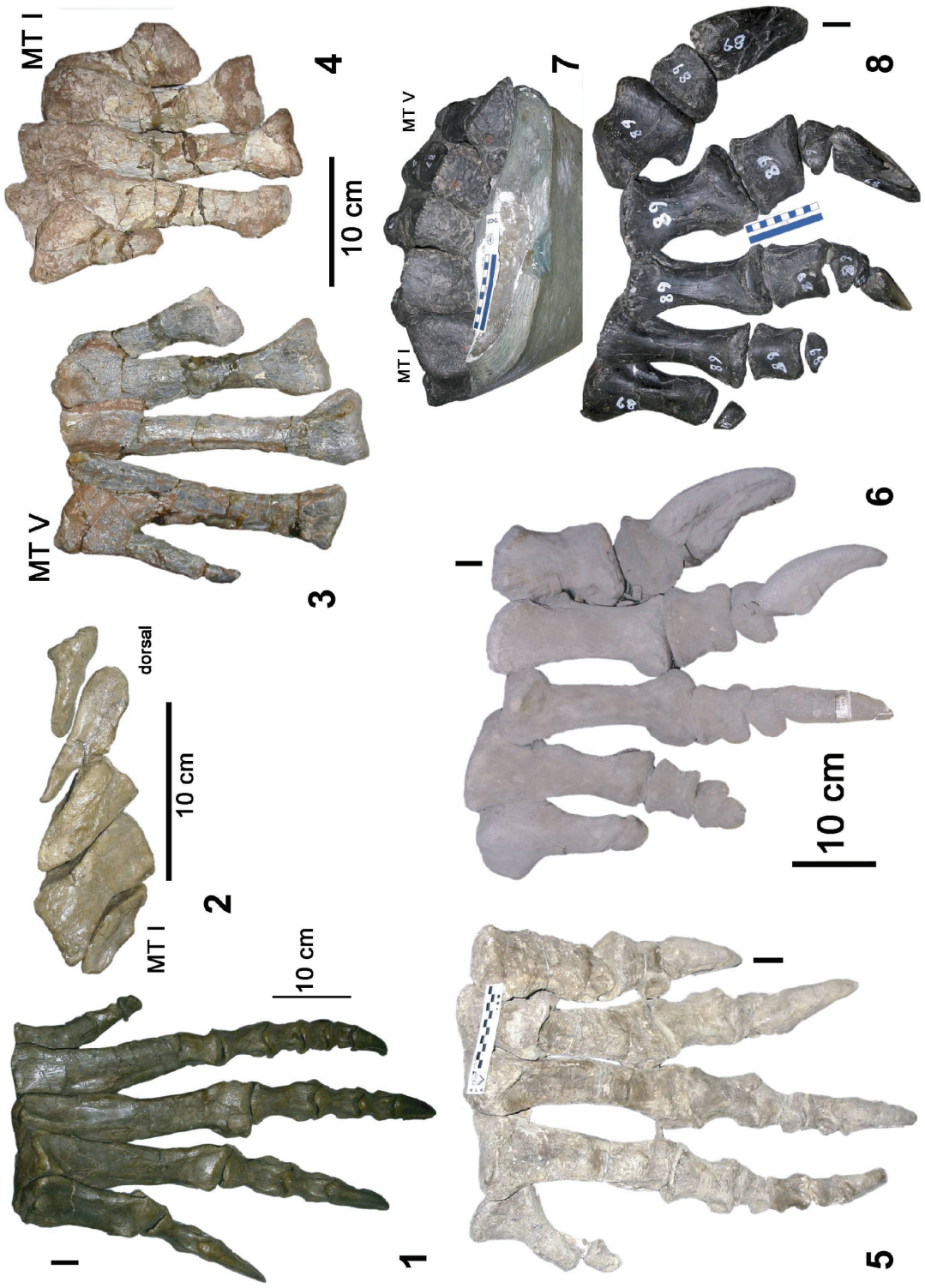

Figure 5.11 *Pes* of sauropodomorphs: 1 - *Plateosaurus engelhardti* (MD indivi. VI) left manus in dorsal view; 2 - *Plateosaurus engelhardti* (MD indivi. VI) left metacarpals in proximal view; 3 - *Riojasaurus incertus* (PVL 3526) left metacarpals in dorsal view; 4 - *Coloradisaurus brevis* (PVL 5904) left metacarpals in dorsal view; 5 - *Jingshanosaurus xinwaensis* (LFM LFM 003.1) left manus in dorsal view; 6 - *Omeisaurus tianfuensis* (ZDM 5005) right manus in dorsal view - scale bar - 10 cm; 7 - *Apatosaurus excelsus* (CM 89) right metatarsals in proximal view - scale bar - 10 cm; 8 - *Apatosaurus excelsus* (CM 89) right manus in dorsal view. Abbreviations: I - digit I; V - digit V; MT I - metatarsal I; MT V - metatarsal V.

Chapter 6 - Sauropodomorph Limb Disparity and Morphospaces

"What is the ultimate limit to the size of land animals? Unfortunately, we are unable to give an adequate answer, and we cannot study the question by building a bigger elephant."

Knut Schmidt-Nielsen*, Journal of Experimental Zoology,* Scaling in Biology: The Consequence of Size (1975, p. 291)

". . . to the scientific mind the living and the non-living form one continuous series of systems of differing degrees of complexity. . . , while to the philosophic mind the whole universe, itself perhaps an organism, is composed of a vast number of interlacing organisms of all sizes."

James G. Needham, *Quarterly Review of Biology,* Developments in Philosophy of Biology (1928, p. 79)

6.1 Summary

The present chapter will focus on the limb proportions of various groups of Sauropodomorpha exhibiting different fore and hind limb specializations as well as distinct sizes. Special attention will be given to limb disparity and morphospace occupation of these taxa, as well as the degree of integration of limb elements and among limbs.

The mean A.D. has been calculated for each group individually (INTRAD), as well as for the super groups that result from the combination of different taxa. All of these computations have been performed in order to evaluate the significance of limb disparity according to the classification used (i.e., paraphyletic groups). The A.D. of super groups (INTERAD) has also been computed as a whole (such as for instance macronarians), that is to say, gathering as much as possible all the members that belong to a natural group, in order to explore the phylogenetic value of limb proportions within Sauropodomorpha. Both levels of computation are depicted in tables 6.2, 6.3, 6.4, 6.5, 6.6 and 6.7.

Disparity metrics is also a way to evaluate the degree of variation of limb proportions among groups. Stasis in limb proportions is a way to undertake possible constraints in appendicular morphology. For the sake of evaluating such a constraint size has been also considered, that is, whether a specific individual A.D., and therefore its positioning within its group proportions morphospace, is related with the absolute length of the bone parts and, if so, determine the association. The initial question is to explore if size in that particular giant taxa do show more or less limb variation. Further analyses cope with recognizing which elements are major sources of variation in limb proportions. Biplot analysis has been used for that purpose. Finally, the balanced variation between elements was explored in order to detect relevant and more integer patterns of variation among Sauropodomorpha groups.

Both the morphological characterization of the appendicular skeleton and the functional morphology of the locomotor apparatus of this group have been introduced in chapter 5.

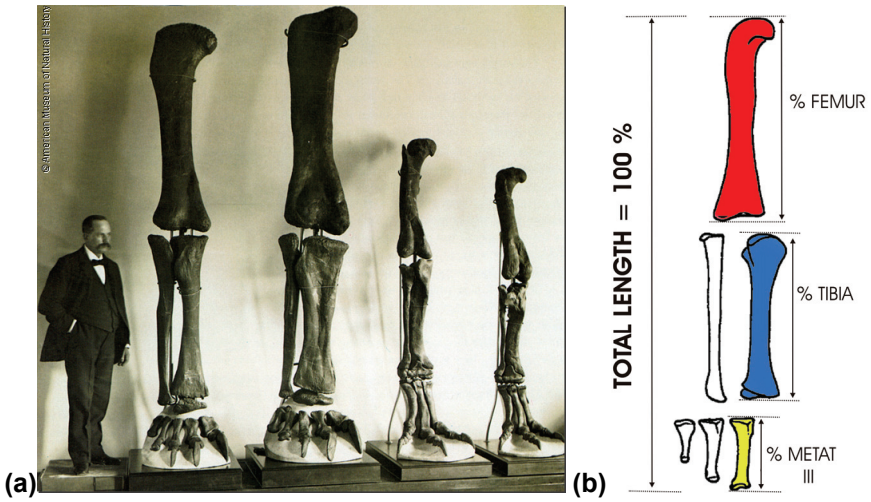

Figure 6.1 a) Hind limb elements of sauropods (two leftmost) and theropods. Adapted from photograph of the American Museum of Natural History. b) Diagram of the appendicular elements in the current analysis. Adapted from Wilson 2005a.

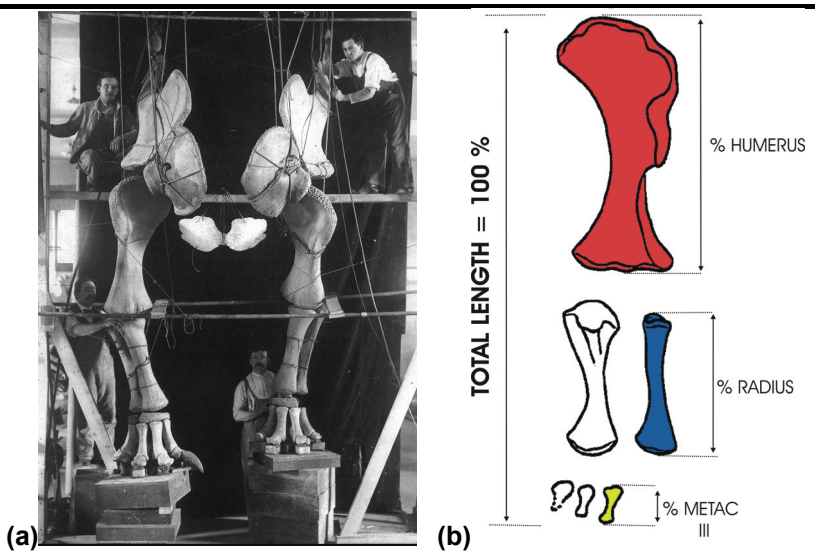

Figure 6.2 a) Fore limb elements of sauropod. Adapted from photograph of the American Museum of Natural History. (b) Diagram of the appendicular elements in the current analysis. Adapted from Wilson 2005a.

Figures 6.1 and 6.2 indicate the generic features of sauropodomorphs both fore and hind limb which will be analyzed herein.

Each limb can be divided into three limb segments: the stylopodium (humerus and femur), zeugopodium (radius and tibia) and autopodium (metacarpal III and metatarsal III). The total limb length and length of each limb segment were either directly measured or obtained from the literature. This way, a tripartite limb with the proportional length for each segment has been constructed.

6.2 Materials

The sauropodomorph sample includes several groups – detailed groups description in chapter 5 and in figure 6.3. These groups will be designated in the following analyzes as “groups” because, from a phylogenetic perspective, they represent paraphyletic grouping. In some specific analyses herein performed, samples have been used that result from the assembly of “groups”, and in these particular cases some may represent monophyletic grouping. These assembled groups will be designated as “super groups. The justification for employing super groups lies mainly in sample size, that is to say, in an attempt to reduce the statistical constrains due to the reduced sample size. Additionally, some of the super groups’ analyses allow investigating the evolutionary history of sauropodomorphs with a broader perspective.

For text readability the following terminology has been employed, except where specifically stated: the group that includes non-eusauropods and non-neosauropods will be designated “basal sauropods” and the group that includes basal Macronaria, basal Titanosauria and Lithostrotia will be designated as “macronarians”.

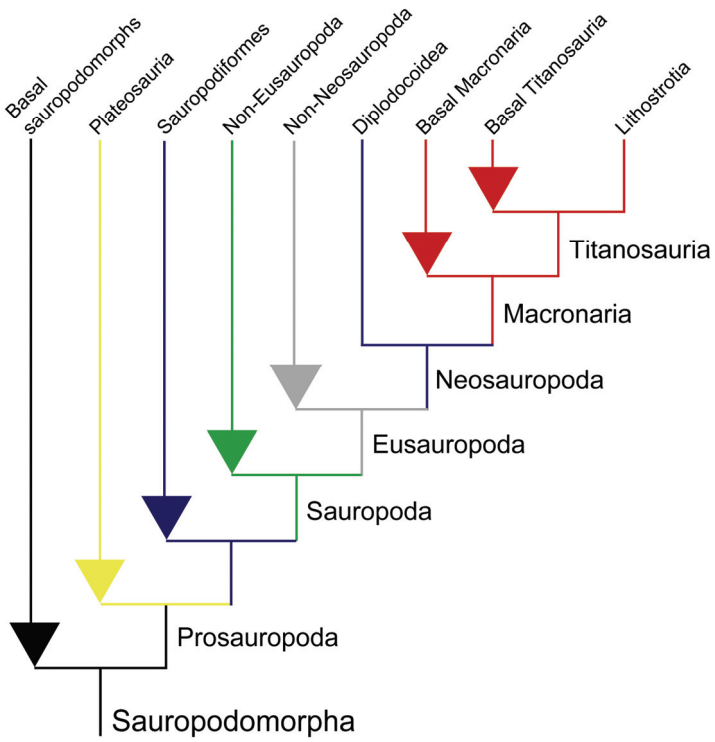

Figure 6.3 Sauropodomorpha generic classification and groups used in this work – nomenclature and ingroup relationships follows the phylogenies described in text and illustrated in figures 5.3 and 5.4. Note that paraphyletic groups are represented in a triangle. Prosauropoda if monophyletic will gather Plateosauria + Sauropodiformes.

6.3 Centroids for fore limbs and hind limbs

Fore and hind limbs centroids (%)	n	H	R	MC	n	F	T	MT
Dinosauromorpha	**1**	40.00	25.71	34.29	**7**	37.74	41.58	20.68
Basal sauropodomorphs+Plateosauria+Sauropodiformes	**(10)**	56.39	32.10	11.51	**(34)**	44.45	37.52	18.03
Basal sauropodomorphs	**0**	a	a	a	**3**	42.00	37.53	20.47
Plateosauria	**5**	56.04	31.22	12.74	**22**	44.78	37.57	17.65
Sauropodiformes	**5**	56.65	32.96	10.39	**9**	44.45	37.36	18.19
Non-Eusauropoda+ Non-Neosauropoda	**(9)**	50.93	35.80	13.27	**(12)**	54.88	34.62	10.50
Non-Eusauropoda	**1**	45.07	41.65	13.26	**4**	53.00	35.24	11.76
Non-Neosauropoda	**8**	51.65	35.09	13.26	**8**	55.79	34.28	9.93
Diplodocoidea	**7**	51.51	34.62	13.85	**6**	55.97	35.05	8.98
Basal Macronaria+Basal Titanosauria+Lithostrotia	**(14)**	51.40	32.49	16.11	**(17)**	56.64	33.99	9.37
Basal Macronaria	**6**	51.47	33.28	15.25	**7**	56.17	35.94	7.89
Basal Titanosauria	**2**	50.68	31.76	17.56	**4**	54.95	36.01	9.04
Lithostrotia	**6**	51.54	31.95	16.51	**6**	55.97	35.05	8.98

Table 6.1 Limb centroids for sauropodomorph groups. a – there are no basal sauropodomorphs with three fore limb bones preserved. Abbreviations: F – femur; H – humerus; MC – metacarpal III; MT – metatarsal III; R – radius; T – tibia.

Analyzing table 6.1 and figure 6.3, one can identify that the plateosaurians, sauropodiformes and basal sauropodomorphs are differentiated mainly in the relative proportion of the analyzed autopodial elements (metacarpal and metatarsal), as well as by the radius proportion*. Concerning the femur proportion, basal sauropodomorphs exhibits a mean value lower than Plateosauria and Sauropodiformes, which are sub-equal. The metacarpal mean contribution to fore limb total length, from Plateosauria to Sauropodiformes, changes from 12.74 to 10.39, that is, decreases by about 2%. The hind limb autopodium part ranges in prosauropods from 17-20% in basal sauropodomorphs and in Sauropodiformes, respectively.

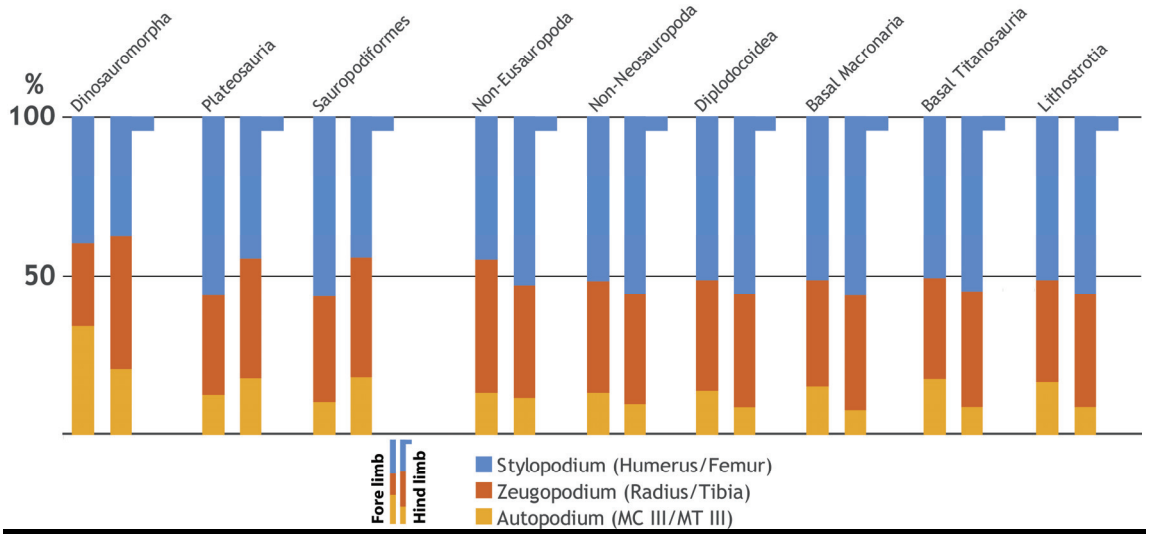

Figure 6.3 Fore and hind limb proportions centroids of dinosauromorpha and sauropodomorphs groups.

The main differences across sauropod fore limb elements lies mainly on the radius and metacarpal mean proportions, given that the humerus mean proportion across sauropod taxa shows equivalent values, ranging from 50.68 to 51.65% in basal Titanosauria and in non-Neosauropoda, respectively. Radius mean proportion in sauropods varies slightly more than the humerus, ranging from 31.76 to 35.09% in basal Titanosauria and in non-Neosauropoda, respectively. Therefore, a general and

* Fore limb proportions were only quantified on Plateosauria and Sauropodiformes due to lack of complete fore limbs of basal sauropodomorphs.

steady reduction in the radius proportion in derived sauropods like macronarians could be observed. An increase of metacarpal mean proportion has been detected, when prosauropods and basal sauropods are compared, and Plateosauria reveal higher metacarpal mean proportion than Sauropodiformes. Sauropod metacarpal mean proportion ranges from 13.26% in non-Neosauropoda to 17.56% in basal Titanosauria, and a general increase in metacarpal proportion along the sauropoda clade could be identified.

Humeral mean proportion reveals a reduction from prosauropods to sauropods in approximately 5%, being the radius proportion equivalent in both prosauropods and sauropods. Among the three fore limb parts, the radius is the element that varies relatively less among both groups of sauropodomorphs, in mean values. It should also be mentioned that radius mean proportion is roughly equivalent in prosauropods and derived sauropods like basal Titanosauria or Lithostrotia.

Prosauropods present an increase in femur mean proportion when one compares basal sauropodomorphs and Plateosauria or Sauropodiformes, ranging from approximately 42% of hind limb length in the former to close to 44% in the latter groups.

Tibia mean proportions are practically identical in prosauropod groups and basal sauropodomorphs, in which it constitutes approximately 37% of the hind limb length. Non-sauropod sauropodomorphs reveal, this way, a very conservative tibia proportion. The biggest distinction in the referred groups hind limb is in the metatarsal proportion, with basal sauropodomorphs revealing around 20% of the limb length and Plateosauria and Sauropodiformes showing nearly 17 and 18%, respectively.

Basal sauropods have a mean femur proportion ranging from about 53 to 55% in non-Eusauropoda and in non-Neosauropoda, respectively. Derived sauropods - e.g., basal Macronaria, basal Titanosauria and Lithostrotia, reveal very similar mean femur proportions that are nearly identical to those of non-Neosauropoda, both fitting in

this same range. Therefore, the femur proportion could be considered as a conservative element in sauropods.

Tibia mean proportions have low variability, ranging from 34.3% in non-Neosauropoda to 36.0% in basal Titanosauria. In general terms, there seems to be an increase in tibia proportion through the Sauropoda clade, with the higher mean value appearing in basal Titanosauria.

Metatarsal proportions are the most variable, similar to what could be quantified regarding the metacarpal. Basal sauropods have higher metatarsal mean proportion than derived sauropods, extreme values being observed in non-Eusauropoda, with close to 12% and in basal Titanosauria, with about 8%. Comparing both sauropodomorph groups, metatarsal is the bone part with the highest range of mean values, decreasing considerably from prosauropods to sauropods.

The hind limb bone proportions of prosauropods could be distinguished from sauropods mainly by the femur and metatarsal mean proportions - prosauropods have relative longer metatarsals and shorter femora than sauropods.

6.4 Limb Morphospaces and Aitchison Distances disparity metrics

If one recalls the concepts of extreme and hybrid forms introduced in section 2.1.2 and compares those concepts with figure 6.4, one can notice that sauropods are stylopodium-extreme forms in both limbs, with the exception of non-eusauropods (represented in the fore limb analysis only by *Vulcanodon*). Sauropods have, therefore, more than half of the total length of each limb in humerus or femur proportions. As described in the next sections, Sauropodomorpha constitutes the only analyzed group in which a single element exceeds half of the total length of the limb. Prosauropods are “stylopodium-extreme” forms only in the fore limb and could be included in the hind limb extreme hybrid forms.

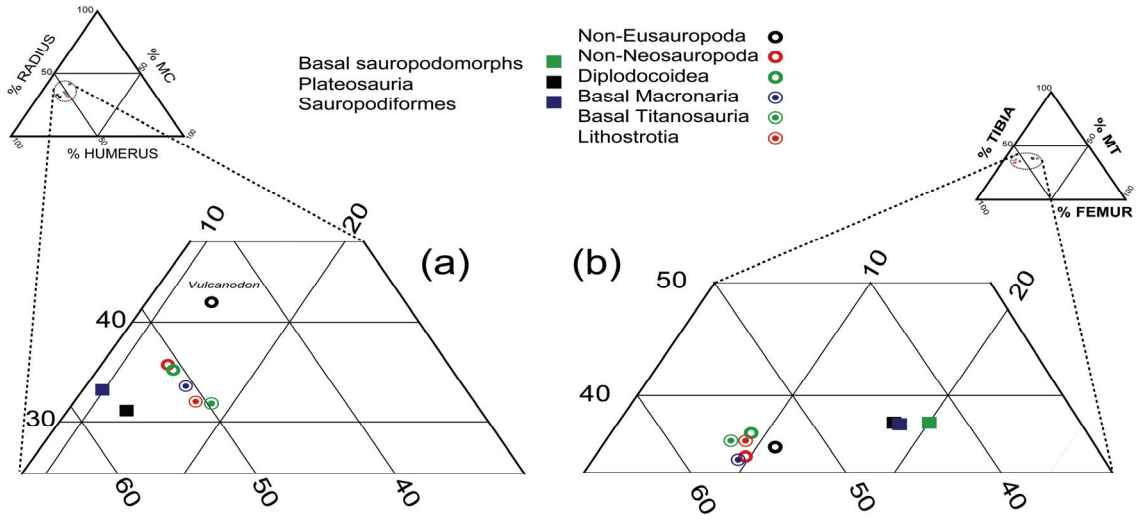

Figure 6.4 a) Ternary diagrams of fore limb and b) hind limb elements of sauropodomorphs groups centroids. Abbreviations: % F – femur percentage; % H – humerus percentage; % MC – metacarpal III percentage; %MT – metatarsal III percentage.

The majority of the groups analyzed in this work[†] are extreme hybrid limb forms, which means that at least one bone part reveals more than 50% of the total limb length.

The above mentioned general trends of group centroids of sauropodomorphs can be observed in figure 6.4, a and b. One detects that in both limb morphospaces prosauropods are clearly separated from sauropods, occupying distinct areas of the morphospaces. These two morphospace areas can be initially defined as “bipedal to facultative quadruped” and “quadruped”, respectively. This denomination is valid when the whole sauropodomorph sample is compared. However, when other dinosaurs and mammalian groups are considered, the morphospace of limb proportions and its locomotion partition is different - see chapter 7.

Prosauropod and sauropod specimens are reasonably separated in the fore limb morphospace and the boundary between the two groups of sauropodomorphs could be established mainly on the basis of the humerus and metacarpal proportions along an axis - see dashed line in figure 6.6. Complementing, one observes that, on

[†] Other non-sauropodomorphs dinosaurs and mammals will be analyzed in chapter 7.

the fore limb morphospace, sauropod groups are differentiated mainly by the radius and metacarpal mean proportions, the humerus proportion remaining rather constant. One could assume the existence of this axis separating prosauropods and sauropods fore limb proportions without the need of performing a centering operation on the data, since the majority of the specimens are placed on a central morphospace and, therefore, are not under the same compositional constraining as if they were placed on the morphospace extremities - recall section 2.2.4.

Morphological differences between the two main groups of sauropodomorphs are more evident in the hind limb than in the fore limb. The apparition of a gap (a non-occupied morphospace area) separating prosauropods and sauropods bigger than the equivalent area in the fore limb morphospace can be stressed. The two groups of sauropodomorphs are differentiated mainly by femur and metatarsal proportions. The sauropods cluster in the hind limb morphospace is different than the fore limb morphospace, since there is a more rounded pattern of occupation reflecting differences in the three limb parts.

6.4.1 Fore limb morphospace

The two groups of sauropodomorphs lie on distinct areas of fore limb morphospace, with an identifiable, although not broad, gap area. Non-sauropod sauropodomorphs occupy, within the morphospace, areas of higher humerus proportions, ranging from 57 to more than 60%, and lower metacarpal proportions, ranging from less than 10% to 15%.

The intermediate bone of the fore limb, the radius, is an element in the fore limb morphospace that does not contribute to the distinction of the two main groups of sauropodomorphs.

Forelimb prosauropod area

Prosauropods fore limb centroids disclose that Plateosauria and Sauropodiformes vary mainly in the radius and the metacarpal, while in the hind limb prosauropod groups show a quite constant tibia mean proportion, being mainly distinguished by the femur and metatarsal proportions.

Figure 6.5 shows that Plateosauria have a more conservative fore limb proportion range than Sauropodiformes, which could be confirmed by the visual analysis of the fore limb morphospace, as well as by the mean intragroup A.D., which will be quantified and analyzed in detail in the next section.

Plateosaur forelimb proportions vary mainly in the stylopodial and zeugopodial elements, that is, the humerus and the radius. *Massospondylus carinatus* (BP/1/5347A) is the most dissimilar species within Plateosauria, with an intragroup A.D. of 0.046 and occupying a closer position to Sauropodiformes in the morphospace, namely *Jingshanosaurus xinwaensis* (LV003, pers. obs. 2006) and *Yunnanosaurus huangi* (IVPP AS V.20, pers. obs. 2006), than to the rest of plateosaurians.

Regarding Sauropodiformes fore limb morphospace area, it can be observed that *Melanorosaurus readi* (NM QR3314) and *Gyposaurus sinensis* (IVPP V.43) are species clearly distinguished from the other prosauropods, with A.D. of 0.139 and 0.090, respectively.

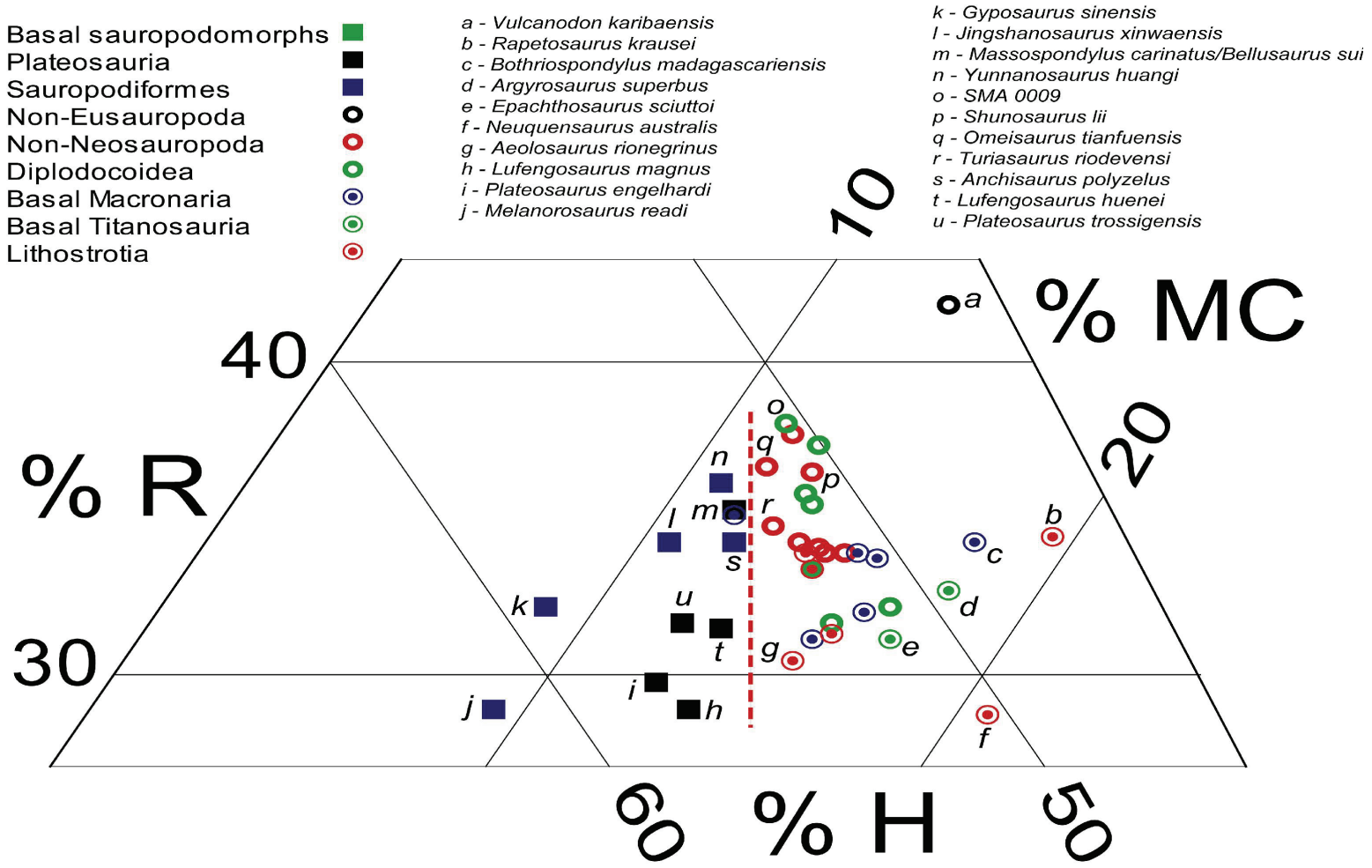

Figure 6.5 Sauropodomorpha fore limb elements morphospace. Some specimens in the morphospace outskirt are identified. Dashed red line represents morphological gap between prosauropods and sauropods - see text. Abbreviations: % H – humerus percentage; % MC – metacarpal III percentage; % R – radius percentage.

Yates (2003a) states that *G. sinensis* should be regarded as a juvenile of *Lufengosaurus*. The fore limb morphospace A.D. of *G. sinensis* to the two species of *Lufengosaurus* does not allow to support Yates (2003a) taxonomical statement. Even though and assuming the juvenile nature of *G. sinensis* one could attribute the cited morphospace dissimilarity to allometry, the A.D. of *G. sinensis* to *Lufengosaurus* is considerable, therefore, should not be regarded as due to phylogeny, but instead to ontogenetic morphological differences. Corroborating this, one could observe the small disparity distance among the related taxa *Lufengosaurus* and *Plateosaurus*, which is considerable smaller than the distance from *G. sinensis* to *Lufengosaurus*. Reisz et al. (2005) stated, based on the morphological analysis of a complete ontogenetic series of *Masspondylus*, that this taxa hatchlings should be regarded as obligate quadrupedal, although altricial, and gave rise to mature facultative bipedal individuals. Both the position in the fore limb morphospace and Reisz et al. (2005) do not support the *G. sinensis* as a *Lufengosaurus* or other taxa juvenile, due mainly to a distant positioning of *G. sinensis* to the quadrupedal area (i.e., sauropods area). In short, it could be stated that:

- the significant fore limb A.D. of *G. sinensis* to the morphospace area occupied by the related taxa *Lufengosaurus* and *Plateosaurus* excludes *G. sinensis* as being close related to *Lufengosaurus*;

- the considerable fore limb A.D. of *G. sinensis* to the quadrupedal morphospace area invalidates the juvenile state of this species.

It could, therefore, be stated that *Gyposaurus sinensis* is a distinct taxa to *Lufengosaurus*. Instead, it can be suggested, by its absolute size and considering it as an adult individual, to be a dwarf prosauropod; or, more plausibly, a juvenile with a distinct allometric trajectory to the prosauropods analyzed by Reisz et al. (2005).

Bellusaurus sui (IVPP V.83003, pers. obs. 2006) has a high percentage of humerus, which places it within the prosauropod morphospace area, with the highest

A.D. to its group centroid - 0.254. This fact could be justified by the early ontogenetic stage attributed to this specimen (Upchurch et al. 2004, p. 265) and not by a morphological resemblance between prosauropods and basal macronarians. This singular prosauropod positioning of a basal macronarian such as *B. sui* could, therefore, be justified only by allometric differences on the appendicular skeleton. It can be, though, speculated that future ontogenetic analysis of limb proportions should be performed in order to evaluate probable appendicular heterochrony. It is relevant that a juvenile sauropod lies on the prosauropod morphospace area. This is contradictory to Reisz et al. (2005), which stated that at least some prosauropods juveniles are obligate quadrupedals that develop bipedality as adults. Thus, it seems that juvenile sauropods have an opposite morphospace placing of juvenile prosauropods, that is to say, in young developmental stages sauropods are close to the bipedal area of the morphospace. This fact could be justified by the ancestral locomotor condition of sauropods, since dinosaurs originated as small-sized, upright bipeds - see chapter 5. Corroborating this, it could also be observed that a diplodocoid juvenile (SMA 0009) reveals high dissimilarity within its group, with an A.D. of 0.120, namely on what concerns the group radius proportion and, although in sauropods area, it is close to the border of prosauropods.

Forelimb sauropod area

Sauropod groups occupy specific areas in the fore limb morphospace, although there is some overlapping. The single non-eusauropod specimen - *Vulcanodon karibaensis* - lies considerably separated from the rest of the sauropods, occupying the most extreme radius proportion position. It could not be assessed if that fact is due to a morphological specificity of this species or a morphometric inaccuracy in the original description work, since the lack of further non-eusauropod specimens invalidates the estimation of this group's limb proportions range. Non-neosauropods

develop a well limited cluster even if this group of sauropods occupies a similar morphospace area as diplodocoids. The non-neosauropod species which are recognizable as being more dissimilar within its group are *Patagosaurus fariasi* (PVL 4076), with A.D. of 0.113 and located in the group lower femur proportion area; and *Omeisaurus tianfuensis* (IVPP T5704 and ZDM T5701/5005), with A.D. of 0.127 and 0.125 located in the group upper radius proportion and group higher femur proportion areas, respectively.

The diplodocoid sample is relatively dispersed considering its size and, as said, is nearer to non-neosauropods in fore limb morphospace than to other sauropods (macronarians). The most dissimilar specimens within the group are, beside the referred SMA 0009, *Amargasaurus cazaui* and *Diplodocus hayi*, which exhibit A.D. of 0.197 and 0.191, respectively.

Rapetosaurus krausei (FMNH PR 2209) is recognizable as a morphospace dissimilar element, with the lowest humerus proportion within its group, although an A.D. of 0.195 does not allow categorizing it as an outlier – see A.D. outliers section. *Neuquensaurus australis* (CS 1100) presents the highest A.D. of Lithostrotia - 0.246. In contrast, *Aeolosaurus rionegrinus* (MPCA 27100) exhibits the highest humerus percentage within Lithostrotia, thus revealing that this group ranges considerable in the fore limb longer bone, but showing a low A.D. within its group - 0.090. *Brachiosaurus brancai* (HMN SII) presents the lowest radius percentage within basal Macronaria and with an intermediate intragroup A.D. - 0.079.

6.4.2 Hind limb morphospace

Prosauropods and sauropods occupy distinct areas of the hind limb morphospace, with a gap area between the two groups. The two groups of sauropodomorphs are differentiated mainly by femur and metatarsal proportions and the operative expression[‡] of the non-occupied morphospace area could be defined roughly between 47-50% of femur and 13-16% of metatarsal. Similar to what was stated regarding the fore limb, the intermediate limb bone (i.e., tibia) remains a similar pattern among both sauropodomorph groups.

Hind limb prosauropod area

Prosauropods are located mainly in the lower femur percentages, between 40-50%, and higher metatarsal percentages, ranging from 10 to 25%. In what concerns the tibia proportions, prosauropods and sauropods reveal almost identical range.

The embryonic *Mussaurus patagonicus* (PVL 4068) is placed in the center of both Plateosauria and Sauropodiformes clusters, with an A.D. within its group of 0.048. This positioning of *M. patagonicus* seems to imply that the allometric differences within prosauropod limbs referred by Reisz et al. (2005) are not reflected equally in the hind limb parts and in the fore limb.

In the morphospace area corresponding to lower femur proportion, mainly prosauropods such as the basal sauropodomorph *Saturnalia tupiniquim* (MCP 3844-PV), the Sauropodiformes '*Sellosaurus gracilis*' (YPM 2192) and the plateosaurs *Ammosaurus major* (YPM 208) and *Gyposaurus sinensis* (IVPP V.27) were identified, with A.D. within the groups of 0.114, 0.277, 0.257 and 0.314, respectively. On the femur extreme corresponding to higher femur proportions, which is closer to sauropods in hind limb morphospace, one could identify *Plateosaurus robustus* (non identified

[‡] In this context "operative expression" means the numerical definition of the one of more axes that defines the range of a certain morphospace area.

specimen, von Huene 1932 in Raath 1972) and also *Jingshanosaurus xinwaensis* (LV003; pers. obs. 2006), although this species is somewhat distant to sauropods area than the former.

The prosauropod species located in the morphospace corresponding to extreme tibia proportions are, in opposite regions, '*Sellosaurus gracilis*' (SMNS 11838)[§] and *Anchisaurus polyzelus* (YPM 1883). Prosauropod metatarsal extreme values correspond to *Gyposaurus sinensis* (IVPP V.27) and '*Sellosaurus gracilis*' (SMNS 11838). It has already been mentioned that *Gyposaurus sinensis* is regarded as a juvenile of *Lufengosaurus* by Yates (2003a) or, as stated in the fore limb morphospace analysis, as a prosauropod juvenile with distinct ontogenetic trajectory to the prosauropods analyzed by Reisz et al. (2005). If one accepts the juvenile nature of *G. sinensis*, one can conjecture that some juvenile prosauropods are placed in extreme metatarsal morphospace regions. A comparable observation was stated about *G. sinensis* fore limb morphospace position, although in this case the metacarpal presented an extreme lower value. It could also be referred that there is only one prosauropod that lies in the sauropod morphospace area, which is *Euskelosaurus browni*, specimen referred as "Maphutseng Euskelosaurus" (Ellenberger and Ginsberg 1966 in Raath 1972), with an A.D. of 0.597.

[§] This specimen although being included in this work should be regarded with caution since the length of the tibia is bigger of the femur - data from Carrano 1998a.

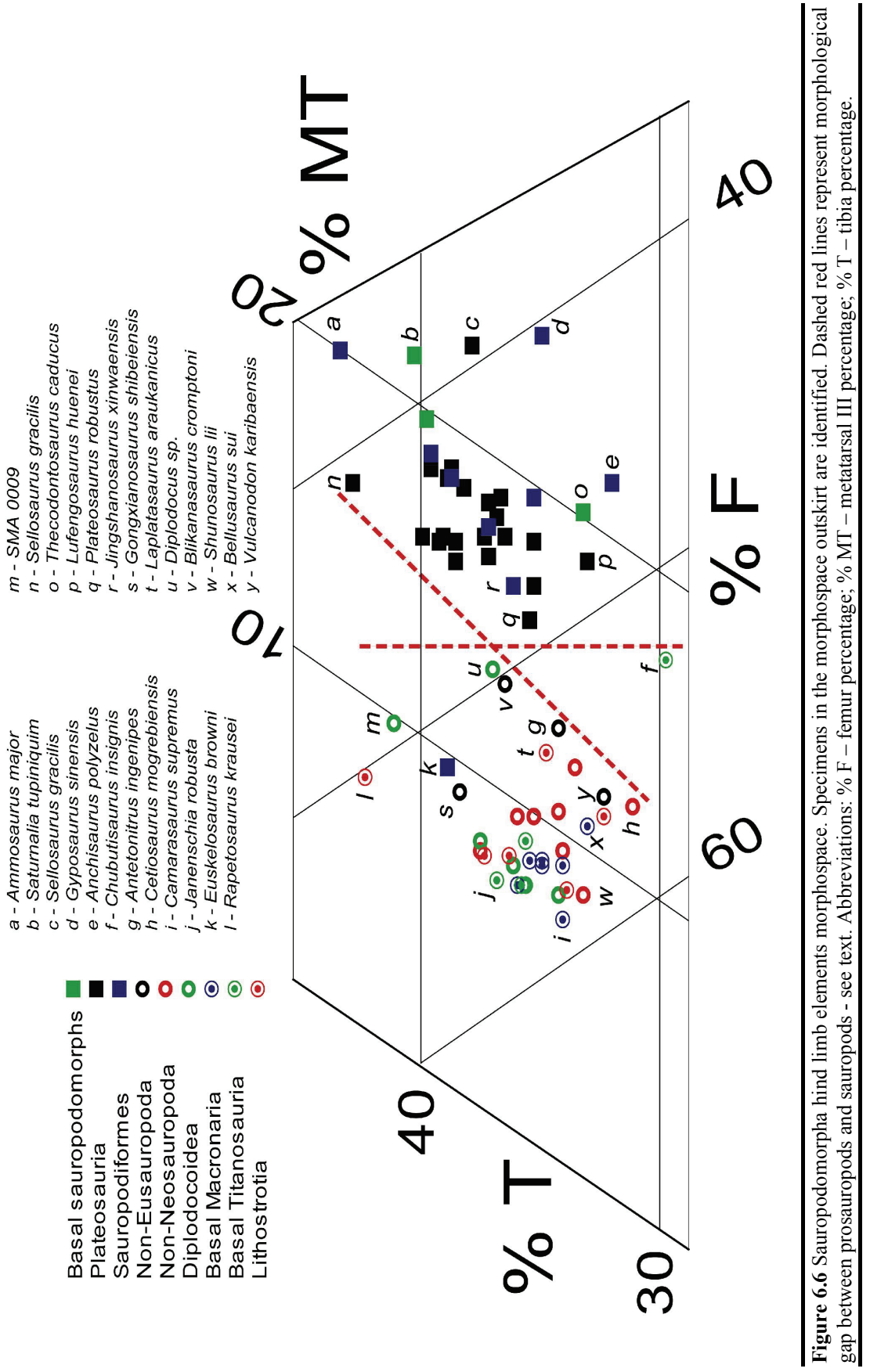

Figure 6.6 Sauropodomorpha hind limb elements morphospace. Specimens in the morphospace outskirt are identified. Dashed red lines represent morphological gap between prosauropods and sauropods - see text. Abbreviations: % F – femur percentage; % MT – metatarsal III percentage; % T – tibia percentage.

Hind limb sauropod area

Sauropods reveal a cluster distinguishable from prosauropods, occupying a morphospace area resultant of higher femur and lower metatarsal proportions than the latter - figure 6.6.

The majority of the non-eusauropod species occupy an area of the morphospace closer to prosauropods, although with distinct femur and tibia proportions among its group. The closest non-eusauropods to the prosauropods area are *Antetonitrus ingenipes* (BP/1/4952) and *Blikanasaurus cromptoni* (SAM K403), the latter revealing one of the lowest sauropod femur proportions[**]. The distant non-eusauropod to the prosauropods referential area is *Gongxianosaurus shibeiensis* (unnumbered specimen, He et al. 1998), with an A.D. of 0.249, it was described it as a sub-adult individual (Wilson 2005a). This high dissimilarity value for *G. shibeiensis* could, therefore, be justified by the ontogenetic stage of this specimen.

Non-neosauropod specimens are placed within a restricted morphospace area and in an intermediate morphospace position between non-neosauropods and the bulk of macronarians, which occupy the higher femur proportion area of the morphospace.

Basal macronarians constitute a well sorted group, although comprising some of the most detached specimens, namely *Camarasaurus supremus* (AMNH 5761), the sauropod species with the highest femur proportion, with an A.D. of 0.215, and *Bellusaurus sui* (IVPP V.83003) with an A.D. of 0.133.

Chubutisaurus insignis (MACN 18222), the sauropod species with the lowest radius and the highest metatarsal proportions, has an A.D. of 0.585. Other two of the most dissimilar basal titanosaur and lithostrotian species are *Ligabuesaurus leanzai* (MCF-PHV-233), with an A.D. of 0.161, and *Laplatasaurus araukanicus* (MLP-Av

[**] *Blikanasaurus cromptoni* femur estimated length published by Galton and Heerden (1998) and cited in Yates (2004).

1047/1128), with an A.D. of 0.259. Similarly to what was stated about the fore limb, *Rapetosaurus krausei* (FMNH PR 2209) is a disparate element within Lithostrotia, with an intragroup A.D. of 0.251.

In general, it could be sustained, taking the cited exceptions into account, that macronarian groups, that is to say, basal Macronaria, basal Titanosauria and Lithostrotia, reveal a well sorted pattern.

Analogously to what was stated regarding *Gyposaurus sinensis*, *Bellusaurus sui* is considered as being a non-adult macronarian and this fact could be the justification for its uncharacteristic position within basal Macronaria morphospace area. Another juvenile sauropod specimen, diplodocoid SMA 0009, reveals an atypical position within the sauropods hind limb area, since it is placed in the lower femur proportions region, with one similar to *Diplodocus sp.* (without reference in Carrano 1998b).

6.4.3 Intragroup Aitchison Distances (A.D.)

The intragroups A.D. (INTRAD) has been computed for the various sauropodomorph groups and for each limb - recall section 2.2.3.

Fore limb

INTRAD reveals that the sauropodomorph group with the most conservative fore limb proportions is basal Titanosauria, as it has the smallest standard deviation (SD), close to zero, followed by non-Neosauropoda, with a SD of 0.036, and Plateosauria, with a SD of 0.053. Nevertheless, this value for basal Titanosauria is not significant and it can be related to the reduced sample size, since there are only two individuals with all fore limb bones preserved, but belonging to two distinct species. In contrast, Lithostrotia is the sauropodomorph group with the highest mean A.D., followed by Sauropodiformes and Diplodocoidea, in decreasing order.

Fore limb intragroups A.D.	N	Me.	Mx.	SD
Plateosauria + Sauropodiformes [1]	**10**	.140	.232	.058
Plateosauria	**5**	.079	.152	.053
Sauropodiformes	**5**	.125	.172	.049
Non-Eusauropoda + Non-Neosauropoda	**9**	.099	.194	.047
Non-Eusauropoda	**1**	**	**	**
Non-Neosauropoda	**8**	.082	.127	.036
Diplodocoidea	**7**	.119	.197	.065
Basal Macronaria + Basal Titanosauria + Lithostrotia	**14**	.120	.309	.086
Basal Macronaria	**6**	.101	.254	.087
Basal Titanosauria	**2**	.035	.035	.000
Lithostrotia	**6**	.147	.246	.071

Table 6.2 Fore limb intragroups Aitichinson distances (A.D.) arithmetic mean (Me.); SD - standard deviation; Mx, – maximum; n - number of specimens; ** - single specimen. 1- Basal Sauropodomorphs does not have any specimen with all three bones preserved.

The difference in A.D. among prosauropod groups could be interpreted as related to the fact that the Sauropodiformes sample includes five genera (*Anchisaurus*, *Gyposaurus*, *Jingshanosaurus*, *Yunnanosaurus* and *Melanorosaurus*), while the Plateosauria sample has only three genera (*Platesoaurus*, *Lufengosaurus* and *Massospondylus*). This taxonomical diversity seems to explain the referred higher Sauropodiformes fore limb disparity.

Among sauropods, there seems to be a general increase in fore limb variability along the clade, although this trend is not linear, since there is a reduction in mean A.D., namely in basal Macronaria and basal Titanosauria. If one combines the individual groups, the general trend of variability increase among sauropods is fully confirmed.

Combining groups and recomputing the mean A.D., one observes that prosauropods fore limb mean A.D. are more disparate than sauropods, and in this latter group basal sauropods exhibit a more restricted occupied morphospace area than diplodocoids or macronarians, which both display equivalent A.D.

Hind limb

The hind limb INTRAD., depicted in table 6.3, shows that the mean A.D. of prosauropods is the least disparate of the combined samples, presenting a mean A.D. of 0.127, followed by basal sauropods, macronarians and diplodocoids, with A.D. of 0.152, 0.163 and 0.172, respectively. One can observe, therefore, that the variability among combined groups increases from prosauropods to sauropods and, in general terms, within sauropods.

Hind limb intragroups A.D.	n	Me.	Mx.	SD
Basal Sauropodomorphs + Plateosauria + Sauropodiformes	34	.127	.589	.112
Basal Sauropodomorphs	3	.117	.167	.048
Plateosauria	22	.088	.277	.059
Sauropodiformes	9	.198	.597	.179
Non-Eusauropoda and Non-Neosauropoda	12	.152	.285	.076
Non-Eusauropoda	4	.146	.249	.069
Non-Neosauropoda	8	.124	.244	.086
Diplodocoidea	6	.172	.377	.103
Basal Macronaria+Basal Titanosauria+Lithostrotia	17	.163	.631	.146
Basal Macronaria	7	.181	.586	.175
Basal Titanosauria	4	.118	.162	.042
Lithostrotia	6	.181	.259	.078

Table 6.3 Hind limb intragroups Aitichinson distances (A.D.) arithmetic mean (Me.); SD - standard deviation; Mx, – maximum; n - number of specimens.

If the non-sauropods sample (i.e., basal sauropodomorphs, Plateosauria and Sauropodiformes) is decomposed in its constituents and the A.D. of its sub-groups are computed, it can be verified that the mean A.D. for Plateosauria is smaller than for Sauropodiformes, thus revealing a lower limb disparity of Plateosauria compared to Sauropodiformes, despite the bigger sample size of Plateosauria.

Within prosauropods, Plateosauria reveal a mean A.D. of 0.088, also with a small SD (the second lowest of the sample), followed by basal sauropodomorphs, with mean A.D. of 0.117, and with the lowest SD of the sample, and Sauropodiformes, with an A.D. of 0.198. One detects that basal sauropodomorphs and Plateosauria exhibit a conservative pattern in the hind limb proportions.

Among sauropods, the least variable groups are basal Titanosauria and non-Neosauropoda, with mean A.D. of 0.118 and 0.124, respectively. If Macronarians are separated in its sub-group elements, and although similar, the mean intragroups A.D. values differ, being higher in basal Macronaria and Lithostrotia, with both groups showing a mean A.D. of 0.181.

Sauropods hind limb A.D. shows a trend of increasement in variability along the clade, although not perfectly linear.

If one analyzes the SD, and takes into account the small sample size of basal Titanosauria, one can state that there is a steady increase in variability along the sauropod clade, ranging from 0.069 in non-eusauropods to 0.175 in basal macronarians.

6.4.4 A.D. Outliers

In the previous section some of the specimens were identified because they were easily recognized in the morphospaces, that is to say, specimens that are detached from its group cluster.

Each individual A.D. to its group centroid was used in order to evaluate the structure of the data and test the existence of outliers (cases with an interquartile range between 1.5 and 3) and extreme values (cases with more than 3 times the interquartile range) through the use of box-plots (Tukey 1977).

Fore limb

One has divided the sauropodomorph specimens into sub-groups and calculated, for each sub-group, its new centroid, which allowed to identify several outliers and extreme values (cases with more than 3 times the interquartile range) concerning the intragroup A.D.

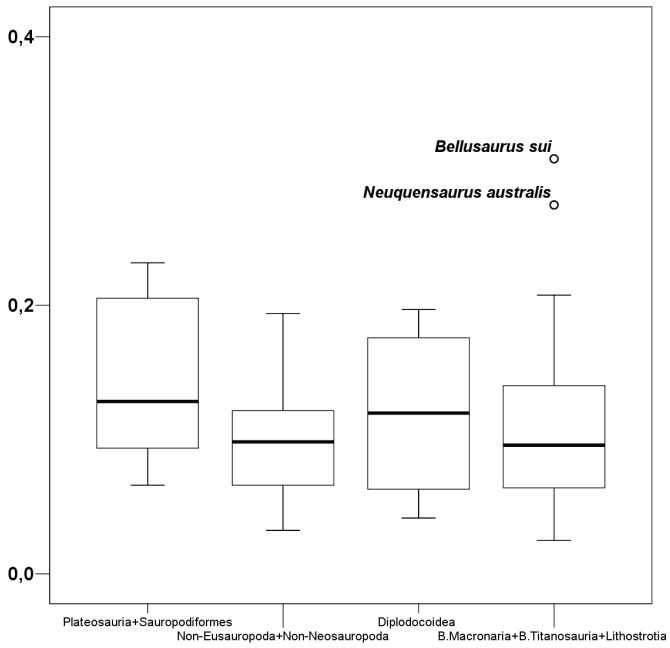

Figure 6.7 Box plot displaying fore limb intragroup A.D.s – outliers are represented as circles. Groups with fewer than two specimens are not shown.

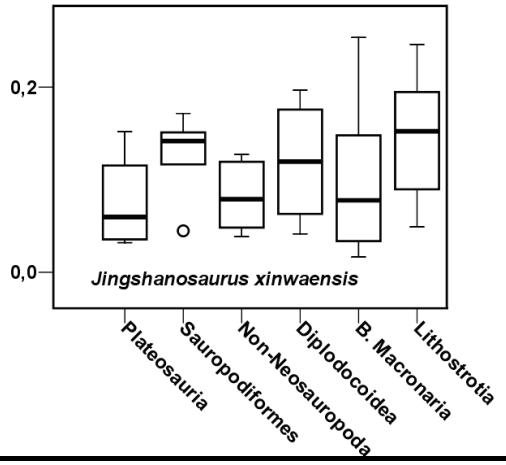

Figure 6.8 Box plot displaying fore limb intragroups A.D. – outliers are represented as circles. Groups with fewer than two specimens are not shown. Note the overlapping in sauropodomorphs with the exception of Sauropodiformes.

Analyzing the groups fore limb A.D., depicted in figure 6.8, it is possible to identify that Sauropodiformes sample reveals one lower outlier, *Jingshanosaurus xinwaensis* (LV003). Despite being considered, in this work, as a Sauropodiformes, fact corroborated by the personal observation of the material (2006), there is still some controversy on the phylogenetic position of this species – see chapter 4. The lower

intragroup A.D. supports, at least for the appendicular skeleton proportions, the Sauropodiformes classification adopted for *J. xinwaensis* in this work.

Among macronarians, two A.D. outliers - *Bellusaurus sui* (IVPP V.83003) and *Neuquensaurus australis* (CS 1100) were identified.

Hind limb

In Plateosauria, there is one extreme value, which is *Sellosaurus gracili*s (YPM 2192). In Sauropodiformes, the atypical specimen is one outlier, *Euskelosaurus browni* (specimen referred as "*Maphutseng Euskelosaurus*" in Raath 1972, table 9) - figure 6.10 - which has been already identified in the intragroup Sauropodiformes A.D. – figure 6.9. In Macronaria, there is one extreme value – *Chubutisaurus insignis* (MACN PV 18222, pers. obs. only on the tibia).

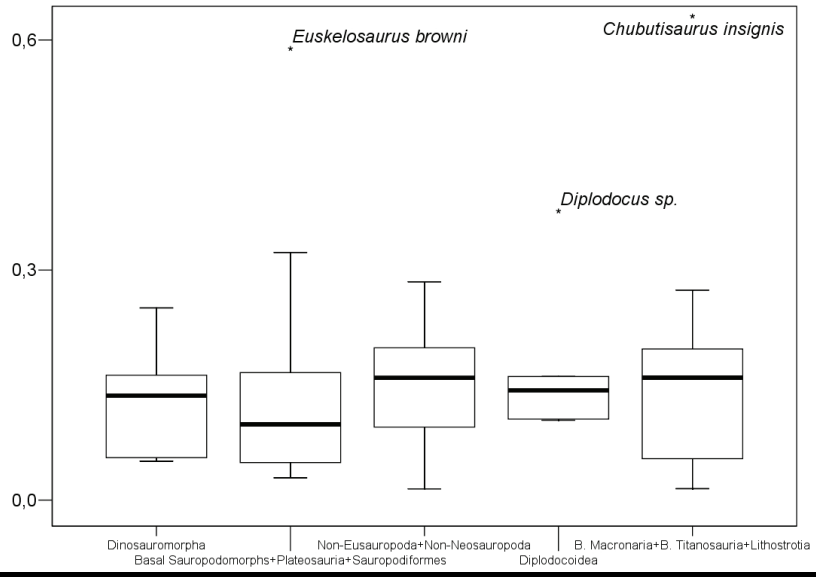

Figure 6.9 Box plot displaying hind limb intragroups A.D. – outliers are represented as circles. Groups with less than two specimens are not represented. * indicates extreme values

Diplodocoidea reveals one extreme value – *Diplodocus sp.* (without reference in Carrano 1998b). Basal Titanosauria fore limb A.D. reveals one outlier – *Chubutisaurus insignis* (MACN PV 18222; pers. obs. 2005).

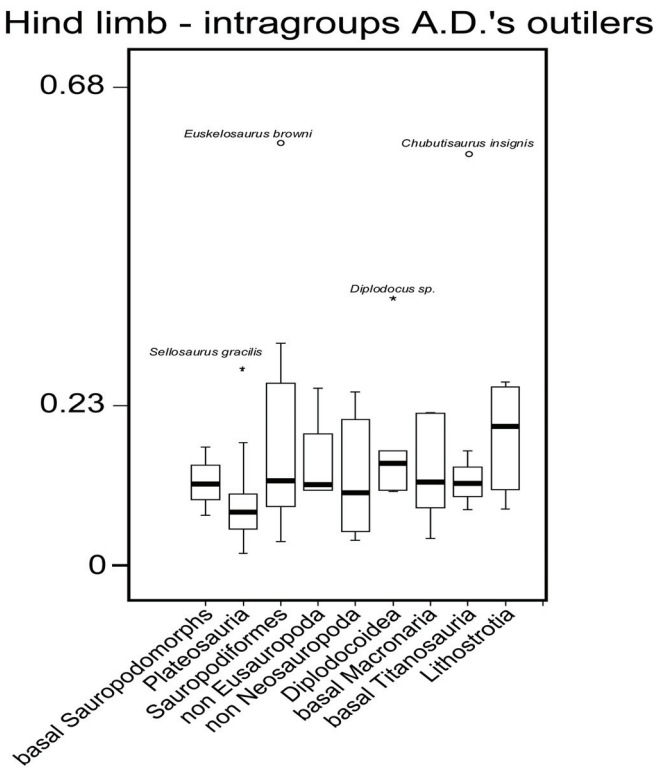

Figure 6.10 Box plot displaying hind limb intragroups A.D. – outliers are represented as circles. Groups with less than two specimens are not represented. O indicates outliers; * indicates extreme values

6.4.5 Intergroup Aitchison Distances (A.D.)

Fore limb

The intergroup A.D. could be defined as the A.D. distance between group centroids[††]. The fore limb intergroup A.D. was computed between the distinct group centroids and is summarized in tables 6.4 and 6.5. Among the numerous disparity indices that could be analyzed in detail from the referred tables, some group relationships were selected, here stated:

-the A.D. among sauropodomorph groups is relatively low, the minimum lying between the basal sauropods and Diplodocoidea (A.D. =0.054), followed by the distance from Diplodocoidea to the most derived sauropods (A.D. =0.156). These

[††] In this section one assumes "A.D." as "intergroup A.D.".

distances could be related to the phylogenetic proximity of Diplodocidea to both cited groups;

- the A.D. from prosauropods to diplodocoids (A.D. =0.196) is somewhat lesser than from basal sauropods to macronarians (A.D. =0.208);

-the A.D. from prosauropods to sauropods increases along the Sauropoda clade, reaching a maximum in Macronarians (A.D. =0.316);

Fore limb A.D.	Plat. + Sps.	N.Eus. + N.Neos.	Diplo.
N.Eus.+N.Neos.	.187		
Diplo.	.196	.054	
B.Macro.+B. Tita.+Lithos.	.316	.208	.156

Table 6.4 Fore limb intergroup A.D.s of combined groups. Abbreviations: Plat.+Sps. – Plateosauria + Sauropodiformes; N.Eus.+N.Neos. – Non-Eusauropoda + Non-Neosauropoda; Diplo. – Diplodocoidea; B.Macro.+B. Tita.+Lithos. – Basal Macronaria + Basal Titanosauria + Lithostrotia.

Analyzing table 6.5, displaying the fore limb A.D. of individual groups, it could be detected that Plateosauria shows a lower A.D. to non-Eusauropoda and non-Neosauropoda or even basal Macronaria than to Sauropodiformes. Sauropodiformes has some of the highest A.D. values among sauropodomorphs, being more distant in the fore limb morphospace to basal Titanosauria and Lithostrotia than, for example, to any basal sauropod group (i.e., non-eusauropods or non-neosauropods).

An A.D. gap between prosauropod groups and basal sauropods is also observable, ranging from 0.358 to 0.382, for Plateosauria and Sauropodiformes, respectively. The fore limb A.D. decreases when comparing prosauropod groups to non-Neosauropoda or Diplodocoidea, both being considerable inferior than the A.D. from prosauropods to non-eusauropods. The morphospace distance from Prosauropoda to Macronaria groups increases, when compared to less derived sauropods, reaching maximum values to basal Titanosauria and to Lithostrotia.

The A.D. between Plateosauria and Sauropoda is lower than the A.D. between Sauropodiformes and Sauropoda. This fact could be justified by the distant positioning of the species *Melanorosaurus readi* (NM QR3314) and *Gyposaurus sinensis* (IVPP V.43) within the Sauropodiformes fore limb morphospace. These species were identified earlier in this chapter as atypical specimens.

	Plat.	Sps.	N. Eus.	N. Neos.	Diplo.	B. Macro.	B. Tita.
Sps.	.196						
N.Eus.	.358	.382					
N.Neos.	.141	.238	.218				
Diplo.	.146	.274	.232	.043			
B. Macro.	.188	.357	.295	.142	.099		
B. Tita.	.308	.492	.401	.283	.241	.142	
Lithos.	.248	.432	.366	.228	.185	.086	.060

Table 6.5 Fore limb intergroup A.D.s. Abbreviations: Plat. – Plateosauria; Sps. - Sauropodiformes; N. Eus. - Non-Eusauropoda; N. Neos. - Non-Neosauropoda; Diplo. – Diplodocoidea; B.Macro. - Basal Macronaria; B. Tita. - Basal Titanosauria; Lithos. - Lithostrotia.

Among sauropods, the groups that show the lowest A.D. are non-Neosauropoda and Diplodocoidea (0.043), the more distant sauropods in fore limb morphospace being non-Eusauropoda and basal Titanosauria (0.401). If one compares all sauropodomorphs, the less dissimilar, that is to say, the ones with lower A.D., are as well non-Neosauropoda and Diplodocoidea, whereas the most dissimilar are Sauropodiformes and basal Titanosauria (0.492).

Diplodocoid sauropods exhibit the lowest A.D. to non-Neosauropoda and to basal Macronaria, being more distant in the fore limb morphospace to basal Titanosauria and non-Eusauropods. These A.D. reveal an intermediate positioning of diplodocoids between basal sauropods and derived sauropods.

A general trend of reduction in fore limb intergroups A.D. is detected along the sauropod clade, because groups that are phylogenetically closer have lower fore limb A.D. than more phylogenetically distant ones.

Hind limb

The hind limb A.D. between combined groups centroids are summarized in table 6.6. The following general disparity relationships among groups can be identified:

- the lowest A.D. occurs among Diplodocoidea and Macronarians (0.060), followed by the A.D. between macronarians and basal sauropods (0.141);
- the highest hind limb disparity indices occur between macronarians and prosauropods;
- the A.D. between macronarians and basal sauropods is greater than the A.D. between diplodocoids and basal sauropods.

Hind limb A.D.	B-Sms. + Plat. + Sps.	N.Eus .+ N.Neos.	Diplo.
N.Eus.+N.Neos.	.536		
Diplo.	.661	.158	
B.Macro.+B. Tita.+Lithos.	.670	.141	.060

Table 6.6 Hind limb intergroup A.D. – B.Sms. + Plat. + Sps. – basal sauropodomorphs + Plateosauria + Sauropodiformes; N.Eus.+N.Neos. - non-Eusauropoda + non-Neosauropoda; Diplo. – Diplodocoidea; B.Macro.+B. Tita.+Lithos. - basal Macronaria + basal Titanosauria + Lithostrotia;

The hind limb A.D. gap between prosauropods and basal sauropods is easily identifiable and reaches its peak between basal sauropodomorphs and non-Eusauropoda - A.D. 0.562.

The A.D. from prosauropods to sauropods follows a general trend, increasing along the sauropod clade. Basal sauropods have lower A.D. to prosauropods than to phylogenetically higher placed sauropods. The A.D. is larger when basal sauropodomorphs and each sauropod group are contrasted, followed by the comparison of Sauropodiformes to the distinct sauropods. The hind limb lowest disparity index is obtained when Plateosauria and each sauropod group are compared.

Among sauropods, the least dissimilar groups in the hind limb morphospace are Diplodocoidea and Lithostrotia, followed by basal Macronaria and non-Neosauropoda. Oppositely, the highest disparity indexes among sauropods occur between non-Eusauropoda and basal Titanosauria (0.359) or between non-Eusauropoda and Diplodocoidea (0.248).

Hind limb A.D.	B. Sms.	Plat.	Sps.	N. Eus.	N. Neos.	Diplo.	B. Macro.	B. Tita.
Plat.	.154							
Sps.	.126	.030						
N.Eus.	.562	.409	.437					
N.Neos.	.721	.567	.596	.159				
Diplo.	.794	.639	.669	.248	.123			
B. Macro.	.773	.619	.647	.210	.052	.102		
B. Tita.	.911	.757	.786	.359	.211	.119	.167	
Lithos.	.791	.637	.666	.238	.101	.029	.074	.121

Table 6.7 Hind limb intergroup A.D. Abbreviation: B.Sms. - basal sauropodomorphs; Plat. – Plateosauria; Sps. – Sauropodiformes; N.Eus. - non-Eusauropoda; N.Neos. - non-Neosauropoda; Diplo. – Diplodocoidea; B.Macro. - basal Macronaria; B. Tita. - basal Titanosauria; Lithos. - Lithostrotia.

The two most dissimilar sauropodomorphs are basal sauropodomorphs vs. basal Titanosauria, followed by basal sauropodomorphs vs. Lithostrotia, with hind limb A.D. of 0.911 and 0.791, respectively.

Although occupying identifiable and specific regions of the hind limb morphospace, sauropods do not reveal a clear trend of A.D. variation within its clade, as identified for the sauropod fore limb. For example, Lithostrotia hind limb A.D. to non-Eusauropoda is maximal, decreasing through the Sauropoda clade until reaching a minimum to Diplodocoidea, as well as increasing to basal Macronaria and basal Titanosauria. Similar A.D. behavior could be identified in basal Titanosauria along the Sauropoda clade, but not in basal Macronaria. This implies that, with the exception of basal Macronaria, there is a trend of A.D. increase when one follows the sauropod clade from the most derived to the most basal forms.

Besides the specific considerations on the above described A.D., the following should be underlined:

- sauropodomorph hind limb A.D. are in general greater than the fore limb A.D., suggesting that sauropodomorphs are more separated in the hind limb morphospace than in the fore limb morphospace;
- prosauropods are more distant to sauropods in the hind limb A.D. than in the fore limb A.D., this morphological difference indicating that the distinct sauropodomorph locomotion patterns are more reflected in the hind limb than in the fore limb.

6.5 Disparity and size

As previously described in chapters 2 and 3, CDA techniques allow comparisons and quantifications of variability among limb element proportions. When one transforms the original data, obtaining compositional coordinates, one removes the absolute size of the variables, also allowing that the statistical difficulties of the unit-sum constraint to be handled.

CDA has been employed herein in order to evaluate and quantify positioning of the specimens and occupation patterns in limb proportion morphospaces.

Aiming to contrast the relationship among the disparity index (A.D.) and absolute size variation within a group, several bivariate correlation analyses on the A.D. of each specimen within its group and the log transformed limb element lengths were performed. These computations were accomplished both in fore limbs and hind limbs elements and across the individual groups.

With the bivariate correlation analyses the goal is to evaluate the role of size in the proportions morphospace disparity indexes (A.D.). In other words, one intends to check whether a specific individual A.D., and therefore its positioning within its group proportions morphospace, is related with the absolute length of the bone parts and, if

so, to identify the association. Therefore, bivariate correlation analyses have been performed on every group and for the log transformed lengths of the humerus, radius and metacarpal, in the fore limb, and of the femur, tibia and metatarsal, in the hind limb. The correlation coefficients, as well as the *p* values of significance, for the analysis with P<0.05, are indicated in table 6.8, as is the signal for the non-significant correlations.

In order to evaluate the influence of juveniles on the contrast of A.D. and size, the non-adults were removed in both limbs samples, the A.D. for the new sample was recomputed and new bivariate analyses were performed - see legend of table 6.8.

The equations with significant correlation coefficients were calculated as depicted in table 6.9.

Intragroups A.D.	**n** fore hind	**H (log length)**		**R (log length)**		**MC (log length)**		**F (log length)**		**T (log length)**		**MT (log length)**	
		r	p	r	p	r	p	r	p	r	p	r	p
Dinosauromorpha	n= 1 n= 7	a	a	a	a	a	a	+	n.s.	+	n.s.	+	n.s.
Basal sauropodomorphs	n= 0 n= 3	b	b	b	b	b	b	.988	.049*	+	n.s.	+	n.s.
Plateosauria	n= 5 n= 22	-	n.s.	-	n.s.	-	n.s.	-.595**	.007*	-.602**	.006*	-.589**	.008
Sauropodiformes	n= 5 n= 9	+	n.s.	+	n.s.	-	n.s.	+	n.s.	+	n.s.	+	n.s.
Non-Eusauropoda	n= 0 n= 4	a	a	a	a	a	a	-	n.s.	-	n.s.	-	n.s.
Non-Neosauropoda	n= 8 n= 8	+	n.s.	+	n.s.	+	n.s.	+	n.s.	+	n.s.	+	n.s.
Diplodocoidea	n= 7 n= 6	-	n.s.	-	n.s.	-.765**	.038*	-	n.s.	+	n.s.	.990**	.001*
Basal Macronaria	n= 6 n= 7	-.801	.028*	-.827	.042	-.862	.027	+	n.s.	+	n.s.	.672 .715**	.034* .036*
Basal Titanosauria	n= 2 n= 4	a	a	a	a	a	a	+	n.s.	+	n.s.	+	n.s.
Lithostrotia	n= 6 n= 6	-.883	.010	-.894	.002	-.903	.014	-.848	.033	-.810	.025*	-	n.s.

Table 6.8 - Correlations of intragroups A.D. and log transformed length of limb parts - see text. *, significant one-tailed; **, analysis with non-adults specimens removed - see specimens removed in text; a, single/two specimen(s); b, no specimens with three preserved parts; n.s., non significant, p>0.05; r, Pearson coefficient; p, p value, significance; +, positive non-significant correlation; -, negative non-significant correlation.

6.5.1 Size and fore limb disparity

All of the following results are summarized in tables 6.8 and 6.9, and also in figure 6.11.

Basal Macronaria and Lithostrotia show significant and strong negative correlations of A.D. and size in all three bone parts. These results imply that bigger individuals of basal Macronaria and Lithostrotia reveal lower A.D., showing therefore lower disparity in the respective groups fore limb morphospace. Diplodocoidea individuals present a non-significant correlation, although revealing a negative signal correlation between A.D. and bone parts length. Larger diplodocoid individuals reveal, this way, lower disparity indices in the fore limb morphospace.

Although there is not sufficient material to evaluate the non-Eusauropoda fore limb, it might be speculated that sauropods reveal two trends in the proportion disparity and size:

I. A direct relationship between A.D. and fore limb bones sizes in less derived sauropods. That is, larger non-Eusauropoda and non-Neosauropoda individuals reveal a wider occupation in the fore limb proportions morphospace than smaller non-Eusauropoda and non-Neosauropoda individuals;

II. In derived sauropods (e.g., Diplodocoidea, basal Macronaria, basal Titanosauria and Lithostrotia), the correlation of A.D. and fore limb bones sizes is opposite to the less derived groups. That is, bigger derived sauropod individuals have lower disparity indices, while smaller derived sauropod forms having lower disparity indices, revealing this way a wider morphospace pattern.

Analyzing the non-significant correlations trends, one could observe that Plateosauria and Sauropodiformes show opposite correlation trends between A.D. and

the sizes of the humerus and radius, but similar signal correlations with metacarpal size.

In order to evaluate the influence of juveniles on the contrast of A.D. and size, in the fore limb sample the following specimens, which are considered as non-adults individuals, were removed: *Gyposaurus sinensis* (IVPP V.43), *Massospondylus carinatus* (BP/1/5347A), the diplodocoid SMA 0009 and *Bellusaurus sui* (IVPP V.83003).

The results obtained on this new sample confirmed the previous ones, that is to say, no significant correlations of A.D. and size were computed in the groups where the non-adults were removed, except in Diplodocoidea, where a strong negative correlation between A.D. and the metacarpal size was identified. This result complements the non-discriminated sample, which suggested a significant and strong negative correlation of disparity index and the bone size in derived sauropods.

A.D. – H	A.D. – R	A.D. – MC	A.D. – F	A.D. – T	A.D. – MT
Basal Macronaria	**Basal Macronaria**	**Diplodocoidea[1]**	**Basal sauropodomorphs**	**Plateosauria[1]**	**Plateosauria[1]**
logH=3.204-2.571*A.D.	logR = 3.007-2.498*A.D.	logMC = 2.520-0.829*A.D.	logF=1.488+5.646*A.D.	logT= 2.718-0.191*A.D.	logMT= 2.402-0.434*A.D.
Lithostrotia	**Lithostrotia**	**Basal Macronaria**	**Plateosauria[1]**	**Lithostrotia**	**Diplodocoidea**
logH=3.256-2.351*A.D.	logR=3.021-2.162*A.D.	logMC = 2.723-3.040*A.D.	logF=2.801-0.195*A.D.	logT= 2.775+1.282*A.D.	logMT= 2.294+0.509*A.D.
					Basal Macronaria[2]
		Lithostrotia logMC=2.641-1.529*A.D.	**Lithostrotia** logF=2.943+1.501*A.D.		logMT=2.043+1.265*A.D.
					logMT=2.158+0.890*A.D

Table 6.9 Equations for sauropodomorphs groups that show significant correlations coefficients at $p < 0.05$ between A.D. and bone parts log transformed lengths. 1 - sample with non-adults removed; 2 - equations fore all sample and non-adults removed samples equations. Abbreviations: F – femur; H – humerus; MC – metacarpal III; MT – metatarsal III; R – radius; T – tibia.

6.5.2 Size and hind limb disparity

As before, all of the following results are summarized in tables 6.8 and 6.9, and also in figure 6.11.

Derived sauropods basal Macronaria and Lithostrotia show a significant correlation of A.D. and bone lengths, namely strong negative correlations in basal Macronaria in the metatarsal length, and Lithostrotia in femur and tibia lengths. Among non-sauropods, only basal sauropodomorphs show a significant and strong positive correlation between A.D. and femur length. The non-significant correlation signals among non-sauropods reveal that basal sauropodomorphs and Sauropodiformes show positive correlation of A.D. and hind limb parts sizes, while Plateosauria show an opposite relationship.

Similarly to what was done in the fore limb sample, the non-adult specimens were removed from the hind limb sample, namely *Massospondylus carinatus* (BP/1/5347A), *Massospondylus carinatus* (BMNH R.8171) *Massospondylus sp.* (PVSJ juvenile), two specimens of *Gyposaurus sinensis* (IVPP V.43 and IVPP V.27), *Mussaurus patagonicus* (PVL 4068), *Ammosaurus major* (YPM 209), *Gongxianosaurus shibeiensis* (unnumbered specimen, He et al. 1998), the diplodocoid SMA 0009 and *Bellusaurus sui* (IVPP V.83003).

In the hind limb and for the all groups, the correlation results remain identical to the complete sample, except regarding Diplodocoidea, in which, after removing the juvenile SMA 0009, a strong positive correlation between A.D. and the metatarsal length could be observed. As for Plateosauria, after removing the non-adults, a strong positive correlation of the A.D. and all the hind limb bones lengths was identified, revealing that Plateosauria individuals with bigger bone parts show bigger A.D.

6.5.3 General trends in size

Both fore and hind limbs morphospaces, as well as the graphical representation of some correlation trends between A.D. and size, are depicted in figure 6.11 and, despite the big number of non-significant correlations of A.D. and sizes among the analyzed groups, it is possible to state that:

- in general, sauropods show an opposite correlation between A.D. and size in the hind limb, except for the primitive and more derived sauropods - non-Neosauropoda and Lithostrotia, respectively. In other words, bigger sauropod individuals present lower disparity indexes in the fore limb of derived sauropods and the opposite relation is observable in primitive sauropods. In the hind limb, only the more primitive (i.e., non-Eusauropoda) and the most derived sauropods (i.e., Lithostrotia) show that bigger individuals have lower disparity indexes; all the remaining sauropod groups reveal that bigger individuals have higher disparity indexes. Derived sauropods show, therefore, a positive correlation of hind limb parts and A.D., that is, bigger derived sauropods show higher disparity indexes in the hind limb morphospace. Accordingly, smaller forms of derived sauropods are more conservative in the occupation of hind limb morphospace. These relationships of A.D. and size are generally the opposite of what was observed and quantified in the fore limb morphospace;

- the general sauropods trend regarding the fore limb relation between size and A.D. is different from the on observed in the hind limb. Primitive sauropods show a direct association of those two parameters, while derived sauropods reveal an inverse correlation of A.D. and size, since significant and negative correlations between A.D. and size were identified for all the three fore limb bone lengths in derived sauropods, as well as in Diplodocoidea metacarpal length. It is therefore acceptable to suggest that, based on the correlation of A.D. and fore limb bones sizes, sauropods have two

distinct fore limb disparity patterns: bigger primitive sauropods are more disparate in the fore limb morphospace, while bigger derived sauropods are more conservative in the fore limb morphospace;

- in non-sauropod groups, it was identified that in the humerus and radius, as well as in the hind limb parts, there is an opposite relationship between A.D. and size, in basal sauropodomorphs and Sauropodiformes, that is to say, bigger individuals reveal higher proportions disparity indexes. Contrarily, Plateosauria bigger individuals reveal lower disparity indexes. The only bone revealing an identical relation between A.D. and size among Plateosauria and Sauropodiformes is the metacarpal, meaning that bigger individuals have lower disparity indexes. This distinctive association of A.D. and bone parts sizes in Plateosauria and Sauropodiformes allows us to say that prosauropods call for two modes of morphospace exploration: Plateosauria smaller forms are more conservative, while Sauropodiformes smaller forms are more disparate, in the proportions morphospaces;

- concerning Lithostrotia, and based on the significant correlations, this group shows inverse correlation of A.D. and size in all bone parts, that is to say, bigger lithostrotian individuals show smaller disparity in limb proportions morphospace, while smaller lithostrotian individuals reveal higher disparity indexes. This fact reveals that smaller lithostrotian occupy wider limbs proportions morphospaces than larger lithostrotian forms. Basal Macronaria and basal Titanosauria show identical correlation relationships in the hind limb, revealing a similar association of hind limb morphospace occupation and size;

- in spite of the insufficient fore limb data in basal Titanosauria, and based on the negative correlation trend of A.D. and size observed in derived sauropod groups, it could be inferred that basal Titanosauria would have identical correlation of A.D. and size, that is to say, an inverse relationship of disparity and size as observable in

diplodocoids and lithostrotians. Therefore, derived sauropods like Diplodocoidea, basal Macronaria and Lithostrotia show opposite correlation signs in all fore limb bones;

- in the hind limb, and regarding only the femur length, prosauropods reveal opposite correlation trends among groups, since in Plateosauria individuals a bigger femur corresponds to lower A.D. and the other two prosauropod groups, although with non-significant correlations, reveal positive correlation signal in the relationship of A.D. and femur size. Plateosauria show identical correlation signs in both the fore and hind limbs, that is, Plateosauria smaller individuals reveal higher disparity indexes. Sauropodiformes demonstrate identical correlation trends in most of fore and hind limb parts. In the stylopodium, zeugopodium and hind limb autopodium, positive correlations of A.D. with the size were identified, while in the metacarpal a negative correlation of A.D. with size could be detected. Therefore, Sauropodiformes with bigger proximal bones, that is to say humerus, radius, femur and tibia as well as the metatarsal have bigger disparity indexes, while Sauropodiformes individuals with smaller metacarpals correspond to smaller disparity indexes.

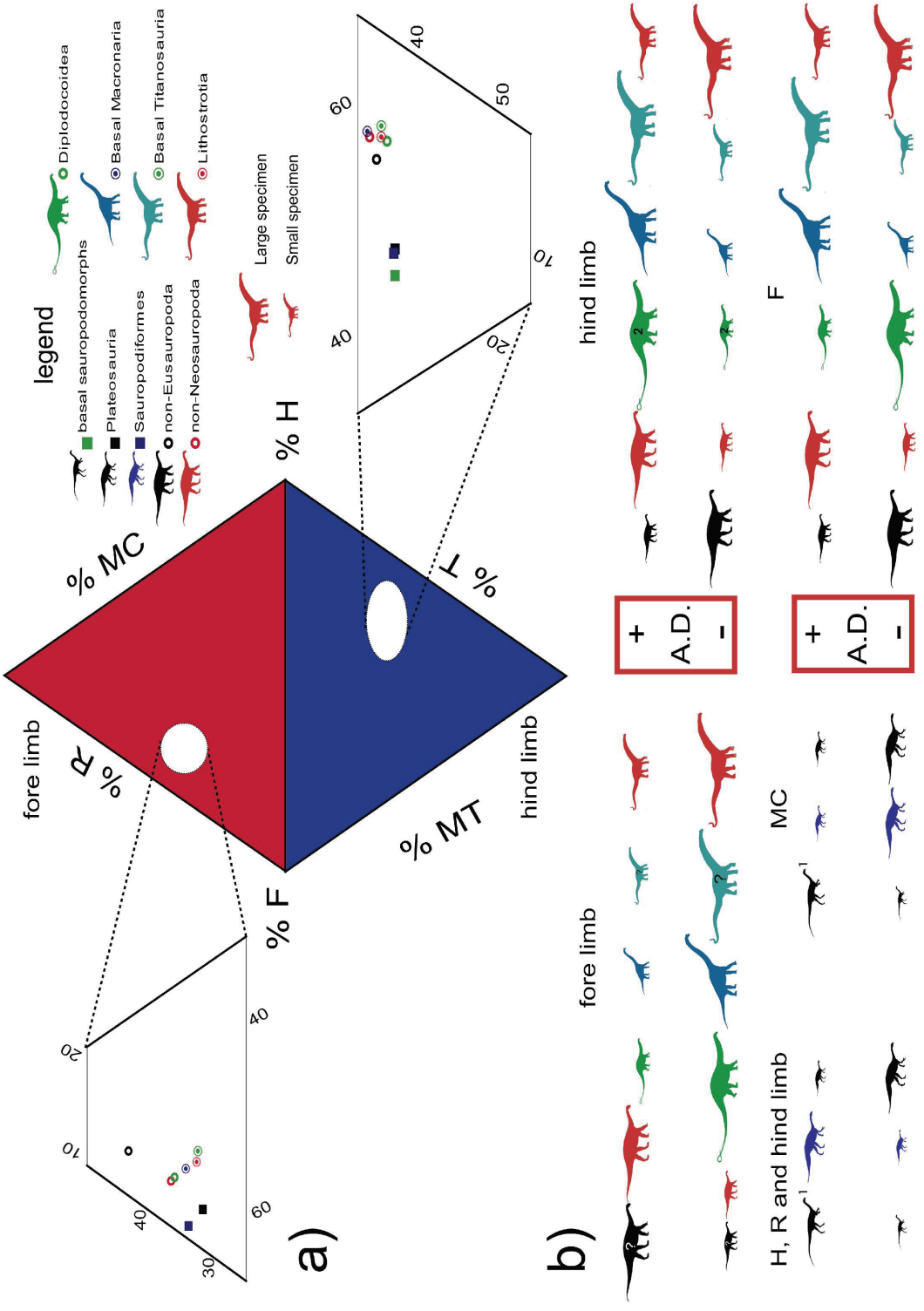

Figure 6.11 a) Sauropodomorphs fore and hind limbs morphospaces with groups centroids. b) Graphical illustration of the bivariate correlations between A.D. and size quantified in table 6.8. Note that the sauropodomorphs silhouettes relative sizes represent absolute bigger and smaller forms. Compare with table 6.8. 1 - Basal sauropodomorphs analysis only in the hind limb; 2 - diplodocoids relationship of A.D. and of tibia and metatarsal sizes only.

6.6 Biplots

Biplots (BP) are descriptive and quantitative statistical tools that are applied to compositional data - see section 2.2.7. BP of limb bone proportions graphically represent patterns of relative variation of the appendicular skeleton parts multivariate data set by projection onto a plane fixed by Principal Components (Aitchison 1990).

This section starts by calling back a BP from section 2.2.7 in order to evaluate the relative variation of Sauropodomorpha hind limb bones - figure 6.12 a and b. It was briefly introduced in chapter 2 that, although there are some general resemblances, the individual BP of prosauropods and sauropods reveal distinct morphological realities: one with the amount of explained variance by the principal axis (PC1), which is larger in sauropods biplot; additionally, the total variance of the sauropod sample (0.127) is considerably larger than the prosauropod sample (0.012).

In both sauropodomorphs BP metatarsal III is the principal source of variability and influences more directly sauropod PC1 than the corresponding axis of prosauropods. Note that tibial control on the total variation is bigger within sauropods than within prosauropods, since the femoral influence surpasses the influence of the tibia. This fact is corroborated by sauropodomorphs six bones parts variation array - table 6.10.

Concerning group discrimination through principal components, and despite the considerable groups clustering, it is possible to state that PC2 of Prosauropoda biplot roughly allows separating Plateosauria from Sauropodiformes and basal sauropodomorphs.

Concerning the atypical species identification, the BP corroborates both the hind limb morphospace and the A.D. previous identifications.

In summary, it could be stated that:

- metatarsal III is the main source of variation both in prosauropods and sauropods;

- tibia is the second most important factor for the total variation in prosauropods, while it is the least important factor in sauropods;

- sauropods sample reveals more total variance than prosauropods sample.

Prosauropod and sauropod fore limb proportions biplot was computed - figure 6.13. PC1 explains 79% of the total variance and is mainly influenced by the metacarpal III. Both humeral and radial proportions have sub-identical control on the total variation - variances of 0.0107 and 0.0105, respectively, for a total variance of 0.0372.

Prosauropoda and Sauropoda fore limb and hind limb parts variances were calculated, and the results are depicted in table 6.10. This analysis was performed in order to confirm the results of the analysis of the six limb parts, because with the partial analyses (i.e., fore limb and hind limbs individual analyses) one could increase the sample size. The results above observed corroborate most of the results of the six bone parts analysis, except in the prosauropods humerus and metatarsal - compare tables 6.10 and 6.11.

The total fore limb variance of sauropods is slightly bigger than the total variance of prosauropods. As above described, the bone part which controls most of the variation is the metacarpal III. It is important to mention that, while in prosauropods both the humerus and the radius proportions present similar variances, in sauropods the radius is more influential than the humerus on the total variation.

Table 6.10 also allows to state that the sauropod hind limb (0.045) is much more variable than the prosauropod hind limb (0.029). Prosauropods exhibit more variance in the femur than in the tibia, although the variances of both parts are somehow equivalent. The metatarsal is the hind limb element that shows more variance among the analyzed parts.

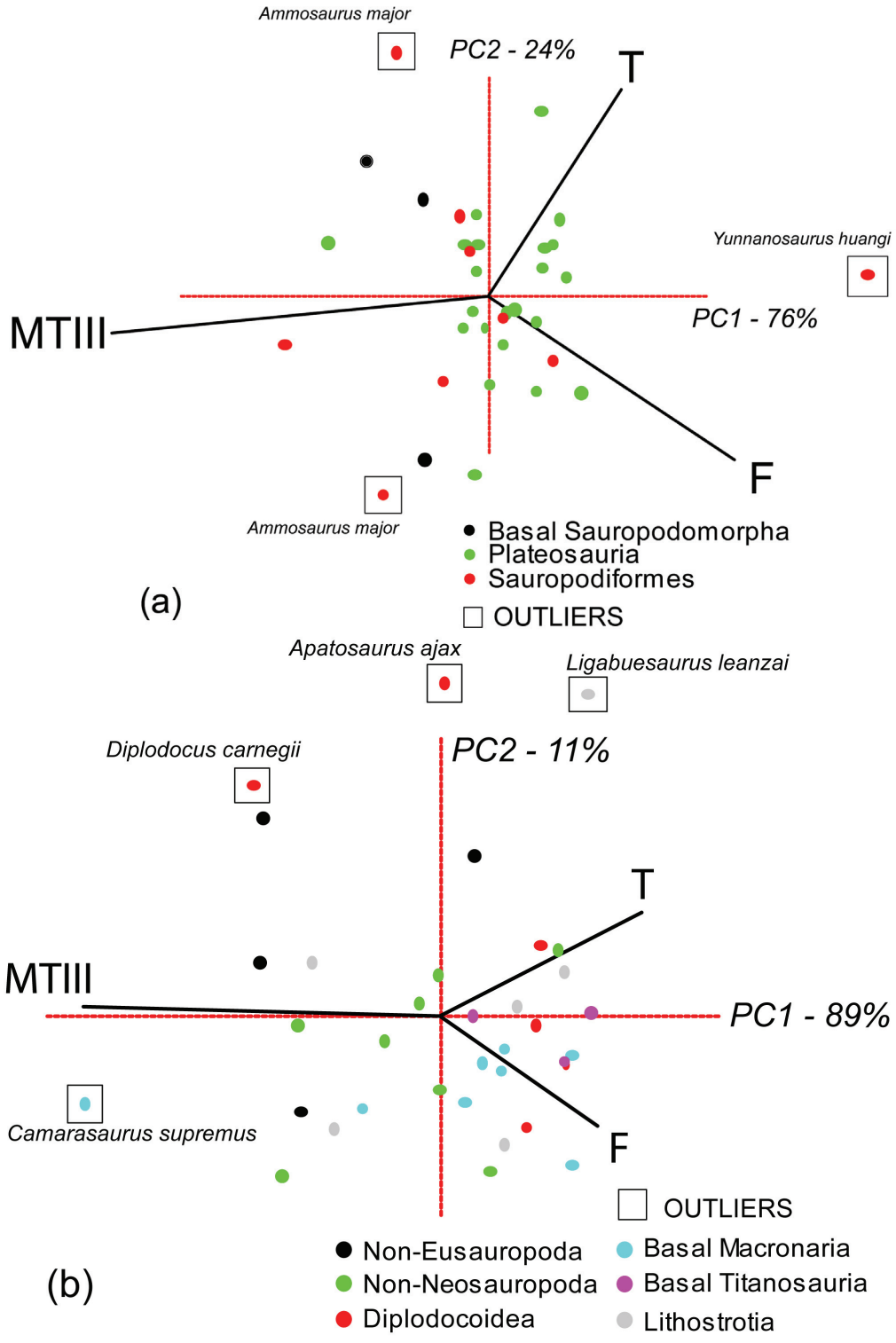

Figure 6.12 a) Biplot of the *clr*-transformed of Prosauropoda hind limb elements – Biplot of the *clr*-transformed space – First Principal Component (76%), Second Principal Component (24%). Abbreviation: F - femur, T - tibia, MTIII - metatarsal III. Outliers - *Ammosaurus major* and *Yunnanosaurus huangi*. b) Biplot of the *clr*-transformed space Sauropoda hind limb elements - First Principal Component (89%), Second Principal Component (11%). F - femur; T - tibia and MTIII - metatarsal III. Outliers - *Diplodocus carnegii*, *Apatosaurus ajax*, *Camarasaurus supremus* and *Ligabuesaurus leanzai*.

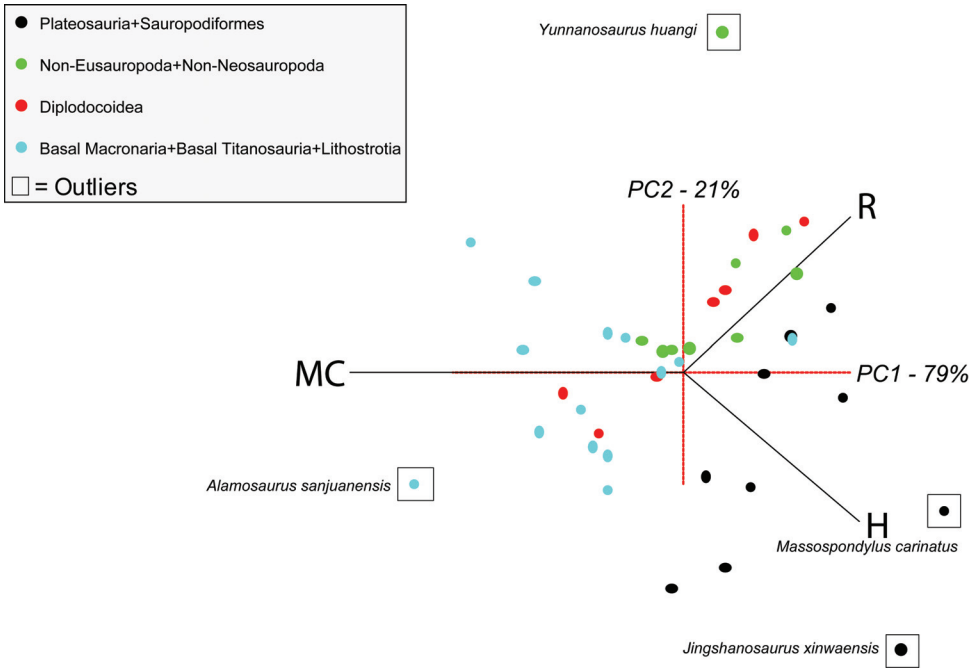

Figure 6.13 Biplot of the *clr*-transformed space of fore limb elements for the first two principal components (PC1 vs PC2) of Plateosauria+Sauropodiformes, Non-Eusauropoda+Non-Neosauropoda, Diplodocoidea, Basal Macronaria+Basal Titanosauria+Lithostrotia,. First Principal Component (79%), Second Principal Component (21%). Outliers – identified in the figure. Abbreviations: H - humerus, R - radius, MC - metacarpal III.

Almost half of the sauropod hind limb variance is due to the metatarsal, the remaining variability being almost equally explained by femoral and tibial variances, although the latter is slightly greater than the former.

Comparing both limbs, it is detectable that the sauropod hind limb shows more variability than the fore limb, while in prosauropods both limbs reveal equivalent variances, despite the differences in sample size among limbs.

Fore	N. Sauro. (n=10)	Sauro. (n=30)	Hind	N. Sauro. (n=34)	Sauro. (n=35)
H	.008*	.006	**F**	.009	.011
R	.008*	.009	**T**	.008	.013
MC	.010*	.012	**MT**	.012	.021
Total variance	.025*	.027	Total variance	.029	.045

Table 6.10 Non-Sauropoda and Sauropoda fore and hind limbs total and bone parts *clr* variances. Abbreviations: H - humerus; R - radius; MC - metacarpal III; N. Sauro. - non-Sauropoda (basal sauropodomorphs, Plateosauria and Sauropodiformes); Sauro. - Sauropoda (non-Eusauropoda, non-Neosauropoda, Diplodocoidea, basal Macronaria, basal Titanosauria and Lithostrotia). *In the fore limb analyses the basal sauropodomorphs were not included due lack of individuals with three bone parts preserved.

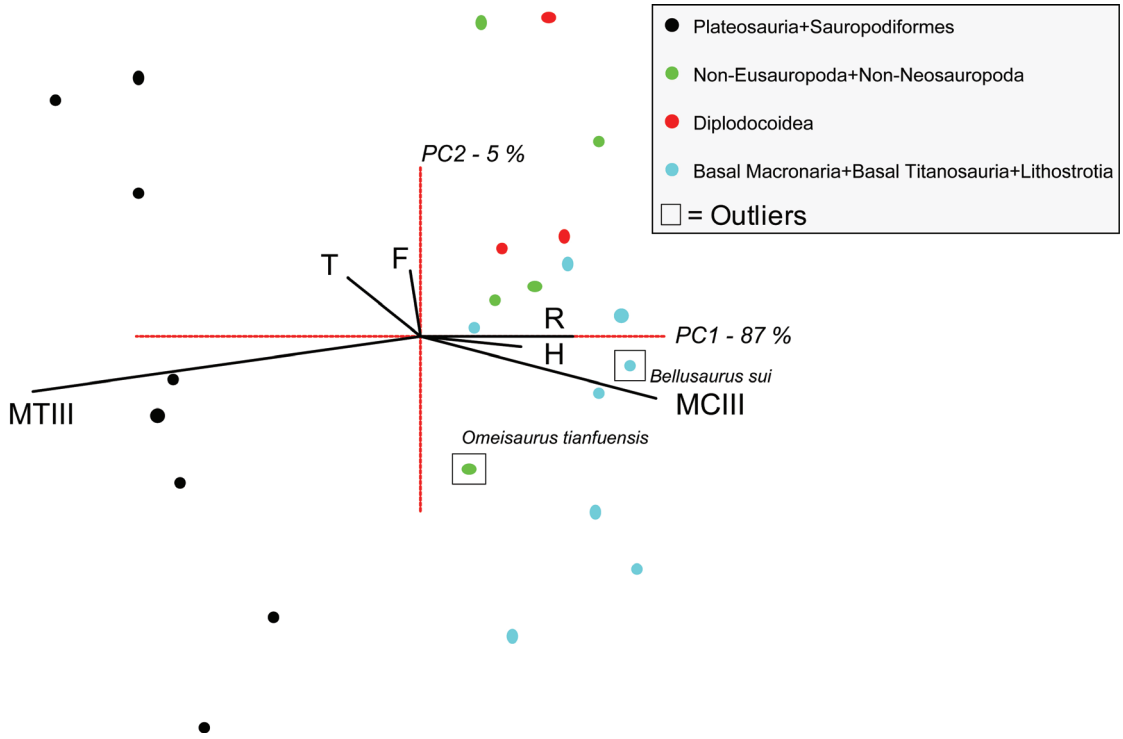

Figure 6.14 Biplot of the *clr*-transformed space of fore and hind limb elements for the first two principal components (PC1 vs PC2) of Prosauropoda (Sauropodiformes and Plateosauria), non-Eusauropoda and non-Neosauropoda; Diplodocoidea; Macronaria (basal Macronaria, basal Titanosauria and Lithostrotia). First Principal Component (87%), Second Principal Component (5%), Third Principal Component (5%), Fourth Principal Component (2%), Fifth Principal Component (1%). Outliers – *Bellusaurus sui* and *Omeisaurus tianfuensis*. Abbreviations: H - humerus, R - radius, MC - metacarpal III, F - femur, T - tibia and MT - metatarsal III.

In order to evaluate patterns of variation, the BP for sauropodomorphs groups six limb parts was computed – see figure 6.14. The first two axes explain 92% of the total variance. PC1 is mainly controlled by the three fore limb bones, humerus, radius and metacarpal, as well as by the metatarsal, which is the main source of variation in the sample. PC1 clearly allows distinguishing non-sauropods and sauropods, while PC2 only discriminates derived sauropods (i.e., basal Macronaria, basal Titanosauria and Lithostrotia) from other sauropod groups. The two most proximal hind limb elements, femur and tibia, have reduced influence on the total variation and determine mainly PC2. It could also be observed that radius and humerus rays are very close, implying that the ratio of those bones is almost constant in the combined sauropodomorphs BP.

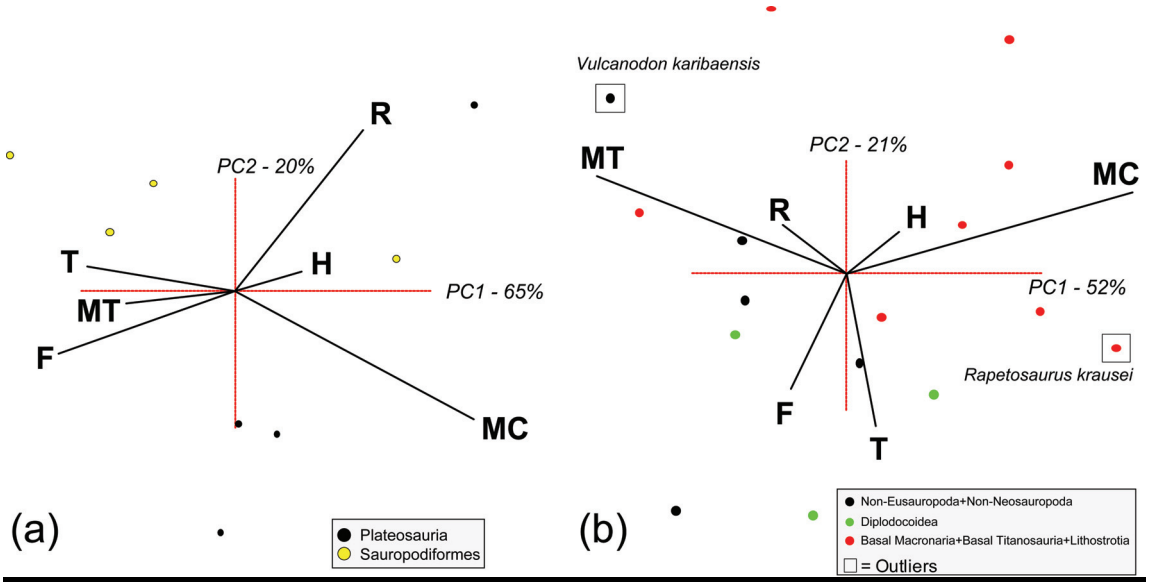

Figure 6.15 a) Biplot of the *clr*-transformed space of the first two principal components (PC1 vs PC2) of Plateosauria and Sauropodiformes. First Principal Component (65%), Second Principal Component (20%). Third Principal Component (10%), Fourth Principal Component (4%) and Fifth Principal Component (1%). There is any outlier. b) Biplot of the *clr*-transformed space of the first two principal components (PC1 vs PC2) of non-Eusauropoda and non-Neosauropoda; Diplodocoidea; Macronaria (basal Macronaria, basal Titanosauria and Lithostrotia), of fore limb elements. First Principal Component (52%), Second Principal Component (21%), Third Principal Component (12%), Fourth Principal Component (10%) and Fifth Principal Component (5%). Outliers – identified in the figure. Abbreviations: F – femur, H - humerus, MC - metacarpal III, MT – metatarsal III, R – radius, T - tibia.

The biplots (figure 6.15 a and b; table 6.11) quantify the relative variation among the six limb parts in both prosauropod groups (i.e., Sauropodiformes and Plateosauria), as well as in Sauropoda groups. The first axis of variation (PC1) in prosauropods sample is controlled mainly by four bone parts: metatarsal, tibia, femur and humerus. Although constituting the four shortest rays, these bones directly influence PC1, explaining 65% of the total variability. The two most variable proportions are the metacarpal and radius, and these bones influence both PC1 and PC2. The second axis explains 20% of total variation among parts. It can be stated that PC2 allows roughly separating Plateosauria from Sauropodiformes specimens and, from what was stated above, the two prosauropod groups could be, therefore, distinguished mainly by the metacarpal and radial proportions.

A probable one dimensional variability is detected in the Plateosauria and Sauropodiformes, due to the geometric configuration of humerus, radius and

metatarsal rays, that is to say, the rays are almost collinear. As seen previously, the inferred one dimensional variability of the referred sub-composition could be confirmed by a principal component analysis of its parts. This sort of analysis is eligible as the scope of future studies.

Variation within the sauropod sample differs from the variation among the parts in prosauropods. PC1 explains approximately half of the total variability and is mainly controlled by the two large rays corresponding to the two autopodial elements (i.e., metatarsal and metacarpal), the latter being slightly more important than the former - table 6.10. PC1 is determined as well by humeral and radial proportions, although at a minor scale. The autopodial bones influence both first principal axes, while PC2, explaining 21% of the total variability, is determined mainly by the hind limb bones, femur and tibia. None of the two principal components axes allow clearly discriminating the sauropod groups.

Prosauropods show more than half of the total variability in the hind limb bones, with the metacarpal proportion representing 25.6% of the group variance (table 6.10). Prosauropods also exhibit equivalent tibial and femoral variances, each of these hind limb bones exhibiting higher variance than the metatarsal.

Sauropods, in turn, show a fore limb as disparate as the hind limb. The two main sources of variability within sauropod individuals are the autopodium bones, which are sub-equal in variance. The humerus and femur represent 12.6% and 13.5% of the total variability, respectively, being somehow equivalent, fact that is not observed in prosauropods, in which the femur proportion reveals bigger variance than the humerus proportion.

Comparing the same bones in the two groups of sauropodomorphs, it is possible to detect that the part showing the most similar variance across the sample taxa is the metacarpal. The major variability differences among prosauropods and sauropods could be identified in the metatarsal, the radius and the femur.

	Prosauropoda (n=8)								Sauropoda (n=16)							
	H	**R**	**MC**	**F**	**T**	**MT**	***clr* var**	**% var**	**H**	**R**	**MC**	**F**	**T**	**MT**	***clr* var**	**% var**
H		.013	.023	.030	.025	.017	.009	**10.5**		.013	.026	.018	.021	.036	.039	**12.6**
R	.536		0.036	.055	.043	.038	.015	**17.4**	.387		.042	.019	.020	.023	.051	**13.0**
MC	1.560	1.025		.070	.070	.058	.022	**25.6**	1.285	.898		.044	.035	.074	.071	**24.5**
F	-.494	-1.030	-2.054		.010	.008	.014	**16.3**	-.282	-.669	-1.567		.013	.027	.035	**13.5**
T	-.234	-.770	-1.795	.260		.018	.014	**16.3**	.155	-.232	-1.130	.438		.039	.039	**14.3**
MT	.416	-.119	-1.144	.910	.651		.012	**14.0**	1.530	1.143	.245	1.812	1.375		.132	**22.1**
	Total variance = .086								**Total variance = .075**							

Table 6.11 Variation array matrices Prosauropoda (Plateosauria andSauropodiformes) and Sauropoda data sets. Abbreviations: H - humerus; R – radius; MC – metacarpal III; F – femur; T – tibia; MT – metatarsal III.

Prosauropod fore limb exhibits more variability than the fore limb of sauropods, which show sub-equal variances in both limbs - table 6.12. The combined variance of autopodial bones is more dissimilar in sauropods than in prosauropods, which is mainly due to the large variance of sauropods metatarsal. Stylopodium and zeugopodium are more variable in prosauropods than in sauropods.

Variance %	**Fore limb**	**Hind limb**	**Stylopodium (H+F)**	**Zeugopodium (R+T)**	**Autopodium (MC+MT)**
Prosauropods	**53.5**	**46.5**	**26.7**	**33.7**	**39.6**
Sauropods	**50.1**	**49.9**	**26.1**	**27.3**	**46.6**

Table 6.12 Combined variances of Prosauropoda and Sauropoda limbs and combined variances of homologous fore and hind limbs parts. Abbreviations: H - humerus; R – radius; MC – metacarpal III; F – femur; T – tibia; MT – metatarsal III.

In this section, the variability among sauropodomorphs limbs was evaluated through the analysis of distinct biplots and the quantification of variance among the bone parts.

Some of the variation patterns that were identified could be resumed as follows:

- sauropods six limb parts total variance is smaller than prosauropods six limb parts total bone parts variance;

- prosauropods hind limb is less variable than sauropods hind limb, while sauropods fore limb is less variable than prosauropods fore limb;

- sauropods hind limb variability is considerably higher than the variability of the fore limb, while prosauropods show equivalent variability when comparing both limbs;

- femur and tibia proportions allow separating derived sauropods from other sauropods;

- stylopodium (i.e., humerus or femur) and zeugopodium (i.e., radius or tibia) proportions are more conservative in sauropods than in prosauropods. Sauropods show bigger variability in the metatarsal than prosauropods, while both groups show equivalent percentages of variability in the metacarpal;

- prosauropods metatarsal is the divergent element within a general sauropodomorphs trend of increase in variability from proximal to distal bones;

- prosauropods are more conservative than sauropods regarding femur and tibia, while prosauropods are more disparate in the humerus and radius.

- prosauropods tibia proportion variance is equivalent to the femur proportion variance, while sauropods tibia variability is bigger than the femur variability;

- sauropods femur proportion variability is equivalent to the humerus variability, while in prosauropods the femur proportion variability is considerably bigger than the humerus variability;

-both sauropodomorph groups hind limb variability is associated mainly with the metatarsal proportion and, at a minor scale, with the femur proportion in prosauropods and with the tibia proportion in sauropods;

- both sauropodomorph groups fore limb variability is associated mostly with the metacarpal proportion and, at a minor scale, with both humerus and radius proportions in prosauropods and with radius proportion in sauropods.

6.6.1 Biplots and size

As seen along this section, biplot analyses are a way to prospect the source of variation on limb proportions. When A.D. analyses and biplot results are crossed, one may have a better approach on what elements are directly affecting the disparity observed in the Sauropodomorpha limbs morphospaces, and how size is involved in the variation. Thus it may be stated that:

1) the study of the bivariate correlations of A.D. and size (sections 6.5.1, 6.5.2 and 6.5.3), as well as the analysis of biplots, allow to establish an adequate and complementary understanding of the proportion variability patterns among sauropodomorphs limb bone parts. The disparity and size analyses discriminate where and how size is influencing the bone proportions variation. The biplots exploration techniques allow identifying and quantifying which parts are varying more, as well as the relation among them.

2) prosauropod fore limb is more variable than the hind limb and the variation is mainly detected in the metacarpal and in the radius parts. To what extent this variation in proportion may affect the morphology is an issue to be explored in future studies, where the application of 3D geometric morphometrics would allow to improve the characterization of the morphological changes occurred in the evolutionary history of sauropodomorphs. Although the bivariate correlation signals of A.D. and size are not significant for prosauropods, it has been noticed that the small influence of size on fore limb disparity is divergent in Plateosauria and Sauropodiformes.

3) derived sauropods present wider patterns of exploration in hind limb morphospace and these patterns are related to size.

4) sauropods reveal higher variation on the hind limb due mainly to the variability of the metatarsal proportion. Additionally, it was recognized that, with the exception of the most primitive and derived sauropod groups, size is directly correlated

with disparity, implying that the larger sauropods are more variable and, from what was initially stated, present more variable metatarsal proportions.

6.7 A.D. Statistical tests

In this work the group differences on two numerical parameters was tested: the disparity index A.D., which offers the information of how group elements are distributed in the morphospace, that is to say, the pattern of specimens distribution in the morphospace; and the compositional data *ilr* transformed, which give information on the location of the group centroid in the morphospace.

6.7.1 A.D. fore limb tests

Two sample t-tests on the A.D. (groups intradistances) for prosauropods and sauropods specimens were applied and it could be stated that there are no significant differences in the pattern of morphospace occupation among the two sauropodomorphs groups, that is to say, there is no significant differences in A.D. group means: t= 1.10; p= 0.296.

An ANOVA test was performed on three sauropod groups (i.e., basal sauropods non-Eusauropoda and non-Neosauropoda; Diplodocoidea; derived sauropods such as basal Macronaria, basal Titanosauria and Lithostrotia) mean intragroups A.D. Based on the ANOVA test it could be said that there are no significant differences in group means A.D.: F= 0.22; p= 0.807. There are no significant differences in the pattern of morphospace occupation among the three groups of sauropods.

6.7.2 A.D. hind limb tests

Two sample t-tests on the A.D. for prosauropods and sauropods specimens were applied and it could be stated that there are no significant differences in the pattern of morphospace occupation among the two groups of sauropodomorphs. There are no significant differences in group means A.D.: t= -1.28; p= 0.206.

A complementary ANOVA test was performed on the three sauropod groups (i.e., non-Eusauropoda and non-Neosauropoda; Diplodocoidea; basal Macronaria, basal Titanosauria and Lithostrotia) mean intragroup A.D. Based on this test, it could be said that there are no significant differences in the pattern of morphospace occupation among the three groups of sauropods. There are no significant differences in group means A.D.: F= 0.07; p= 0.937.

6.7.3 *ilr* MANOVA tests

In order to test group differences, the compositional data has been transformed with *ilr* - isometric logratio transformation - see section 2.2.6; Pawlowsky-Glahn and Egozcue (2001); Egozcue et al. (2003). Since the *ilr* is a transformation of coordinates of a composition with respect to an orthonormal basis, a transformation from the simplex into a real space, all the standard multivariate statistical techniques could be employed on the transformed data. For the three-part composition of a limb, the three representations can be written as a vector with two components *ilr* coordinates. Thus, diverse *ilr* plots were analyzed in order to confirm the differences among fore and hind limb proportions.

Multivariate Analysis of Variance – MANOVA – tests were performed on the *ilr*-transformed coordinates, in order test if there were statistically significant differences among groups limb proportions parameters.

6.7.4 *llr* fore limb

MANOVA indicated highly significant differences in fore limb elements proportions among the six groups means: Plateosauria and Sauropodiformes (n=10); basal sauropods non-Eusauropoda and non-Neosauropoda (n=9); Diplodocoidea (n=7); derived sauropods basal Macronaria, basal Titanosauria and Lithostrotia (n=14); Theropoda (n=11); Ornithopoda (n=12) - Wilks' lambda = 0.245, F[10,112] =11.439, $p < 0.001$.

When the groups are divided in its elements - Plateosauria (n=5); Sauropodiformes (n=5); Non-Neosauropoda (n=8); Diplodocoidea (n=7); basal Macronaria (n=6); basal Titanosauria (n=2); Lithostrotia (n=6); basal Theropoda (n=2); Ceratosauria (n=2); Coelurosauria (n=6); Iguanodontia (n=11) - the differences in fore limb means still remain significant Wilks' lambda = 0.185, F[20,102] =6.750, $p < 0.001$.

6.7.5 *llr* hind limb

MANOVA indicated highly significant differences in hind limb elements proportions among the seven groups means: Dinosauromorpha (n=7); basal sauropodomorphs, Plateosauria and Sauropodiformes (n=34); basal sauropods such as non-Eusauropoda and non-Neosauropoda (n=12); Diplodocoidea (n=6); derived sauropods such as basal Macronaria, basal Titanosauria and Lithostrotia (n=17); Theropoda (n=109); Ornithopoda (n=29) - Wilks' lambda = 0.203, F[12,412] =41,842, $P < 0.001$.

When the groups are divided in its elements - the differences in hind limb means still remain significant - Dinosauromorpha (n=7); basal sauropodomorphs (n=3); Plateosauria (n=22); Sauropodiformes (n=9); non-Eusauropoda (n=4); non-Neosauropoda (n=8); Diplodocoidea (n=6); basal Macronaria (n=7); basal Titanosauria (n=4); Lithostrotia (n=6); basal Theropoda (n=6); Carnosauria (n=16); Ceratosauria

(n=19); Coelurosauria (n=68); Iguanodontia (n=15); non-Iguanodontia (n=14) - Wilks' lambda = 0.110, F[30,394] =26.395, P < 0.001.

6.7.6 Statistical tests final remarks

In the previous sections, both the groups centroids position, informative on the placement within the morphospace, as well as the groups disparity indexes A.D. (group intradistances), which indicates on the distribution of specimens, were tested.

The tests on A.D. allow to state that there are no significant differences in the patterns of specimens distribution among prosauropods and sauropods, both in fore and hind limb morphospaces. A similar result was obtained when comparing the fore and hind A.D. of three sauropod groups - basal sauropods (non-eusauropods and non-neosauropods), diplodocoids and derived sauropods (basal macronarians, basal titanosaurs and lithostrotians).

The absence of a clear distinctiveness in the patterns of distribution of individuals in the studied sauropodomorphs groups seems to imply the existence of phylogenetic constrains, specific of sauropodomorphs, which contributes to the referred morphological disparity homogeneity.

Although the morphospace position of certain groups could be different, its individual pattern of distribution could be identical, thus revealing a similar specimens distribution.

The statistical tests performed on the parts proportions (*ilr*) allow to state that there is a specific position for each group studied, both in the fore limb as well as in the hind limb morphospaces, that is to say, each group occupies a precise area of the morphospace.

6.8 Balances

A theoretical background of balances analysis was introduced in chapters 2 and 3, in which examples of applications were detailed, performed and described. The following partitions of the sauropodomorphs sample have been used in the balances analysis mainly to compare both limbs; allow the comparison among the homologous appendicular modules; perform intra-limb comparisons. The balances are explained in table 6.13.

Balance	Bone parts						Anatomical/Analytical meaning
	H	R	MC	F	T	MT	
B1	**1**	**1**	**1**	**-1**	**-1**	**-1**	fore limb vs. hind limb
B2	**1**	**1**	**-1**	**0**	**0**	**0**	humerus and radius vs. metacarpal
B3	**1**	**-1**	**0**	**0**	**0**	**0**	humerus vs. radius
B4	**0**	**0**	**0**	**1**	**1**	**-1**	femur and tibia vs. metatarsal
B5	**0**	**0**	**0**	**1**	**-1**	**0**	femur vs. tibia

Table 6.13 Sequential binary partition (SBP) used in the balance balance dendrogram illustrated in figure 6.16. Parts: F – femur; H – humerus; MC – metacarpal III; MT – metatarsal III; R – radius; T – tibia.

The computed balances for each sample are as follows:

$$B1 = \sqrt{\frac{3 \cdot 3}{3+3}} \ln \frac{(F \cdot T \cdot MT)^{1/3}}{(H \cdot R \cdot MC)^{1/3}},\ B2 = \sqrt{\frac{2 \cdot 1}{2+1}} \ln \frac{(H \cdot R)^{1/2}}{(MC)^{1/1}},\ B3 = \sqrt{\frac{1.1}{1+1}} \ln \frac{(H)^{1/1}}{(R)^{1/1}},$$

$$B4 = \sqrt{\frac{2.1}{2+1}} \ln \frac{(F \cdot T)^{1/2}}{(MT)^{1/1}}, B5 = \sqrt{\frac{1.1}{1+1}} \ln \frac{(F)^{1/1}}{(T)^{1/1}}.$$

The following table depicts the decomposition of the variances of these balances:

Balance	Plat. + Sps. n= 16		N.Neos. + N.Eus. n= 5		Diplo. n= 3		B.Tita. + B.Macro. + Lithos. n= 8		var total by balance	var % by balance
	var	%	var	%	var	%	var	%		
B1 (fore limb vs. hind limb)	.043	**58.0**	.018	**23.8**	.001	**1.1**	.013	**17.1**	.075	**34.5**
B2 (humerus and radius vs. metacarpal)	.015	**32.3**	.004	**7.8**	.011	**22.0**	.018	**37.9**	.048	**22.0**
B3 (humerus vs. radius)	.006	**29.9**	.007	**34.5**	.004	**20.8**	.003	**14.7**	.020	**9.1**
B4 (femur and tibia vs. metatarsal)	.006	**11.6**	.019	**35.2**	.008	**15.7**	.020	**37.5**	.053	**24.4**
B5 (femur vs. tibia)	.004	**20.3**	.003	**12.4**	.008	**37.8**	.006	**29.5**	.022	**10.0**
var total (by groups)	.075		.050		.032		.060		**Total variance**	
var % (by groups)	**34.7**		**22.9**		**14.7**		**27.7**		**.217**	

Table 6.14 Variance decomposition for each group and respective balances. Variances are indicated as absolute values and percentages for: balance, group and within groups. Balances indicated in table 6.11. Abbreviations: Plat. – Plateosauria; Sps. – Sauropodiformes; N. Eus. - non-Eusauropoda; N. Neos. - non-Neosauropoda; Diplo. – Diplodocoidea; B. Macro. - basal Macronaria; B. Tita. - basal Titanosauria; Lithos. – Lithostrotia.

Balances

The most important balances in terms of variance are B1 (34.5% of the total variance) and B4 (24.4% of the total variance), followed very closely by B2 (22.0% of the total variance) - see table 6.13. These three balances represent more than four fifths of the total variance. The balance with the lowest value of variance (9.1%) is B3 – humerus vs. radius, closely preceded by B5 (10%). Therefore, the balance between limbs explains most of the variance quantified.

Comparing the variability of the balances of homologous bone elements, stylopodium, zeugopodium and autopodium of fore and hind limbs, prosauropods and sauropods are clearly distinguished by B3 and B5. In B3 - humerus vs. radius, a steady reduction in variability among basal sauropod individuals is observed. In B5 - femur vs. tibia, the variability of basal sauropods is smaller when compared to prosauropods. In this balance, a constant reduction in the variability among species within Sauropoda could also be observed.

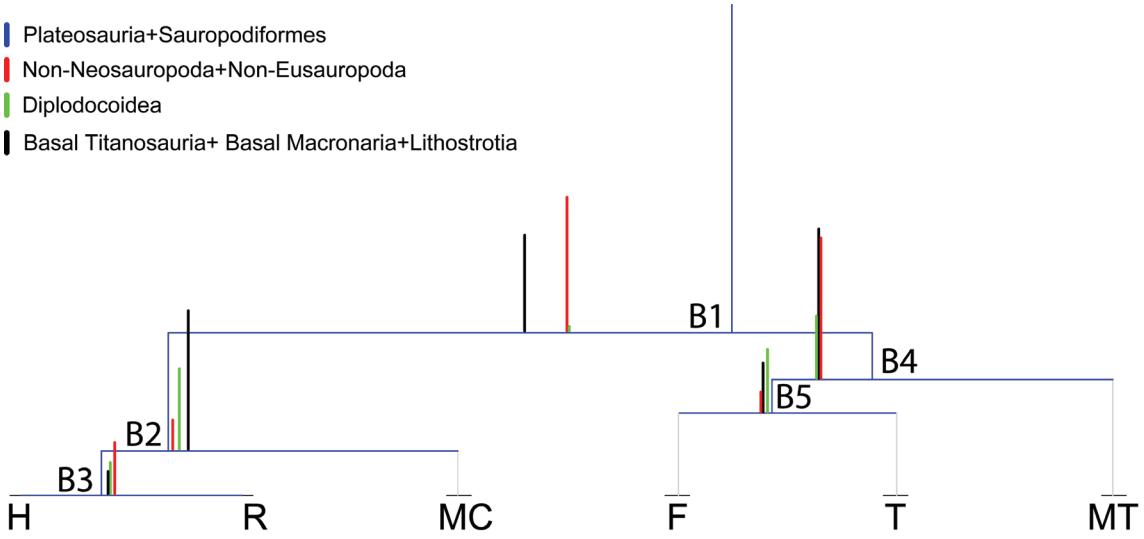

Figure 6.16 Balances dendrogram of sauropodomorphs groups. Sequential binary partition indicated in Table 4.8. Parts: F – femur; H – humerus; MC – metacarpal III; MT – metatarsal III; R – radius; T – tibia.

Regarding B2 and B4 – stylopodium and zeugopodium vs. autopodium, the difference between Prosauropoda and Sauropoda is characterized by a divergent variability modification. In B2 – humerus and radius vs. metacarpal III, the variability increases in sauropods, despite the single exception observed in Diplodocoidea. In balance B4 – femur and tibia vs. metatarsal III, the variance decreases from non-sauropods to sauropods and increases steadily in the latter clade.

In conclusion, some trends can be identified in the analyzed balances, namely the opposite variability trend between prosauropods and sauropods, regarding both fore and hind limb homologous elements. Regarding only the fore limb elements balances - B2 and B3, the trends are a reduction in variability among taxa in B2 and an increase in variability in B3, from non-sauropods to sauropods. Oppositely, for hind limb balances – B4 and B5, the trends are an increase in variability in B3 (i.e., humerus to radius) and a decrease in B5 (i.e., femur to tibia), when comparing prosauropods and sauropods. It should be mentioned that the referred reduction in variability in the ratio of humerus to radius is steady among the Sauropoda clade.

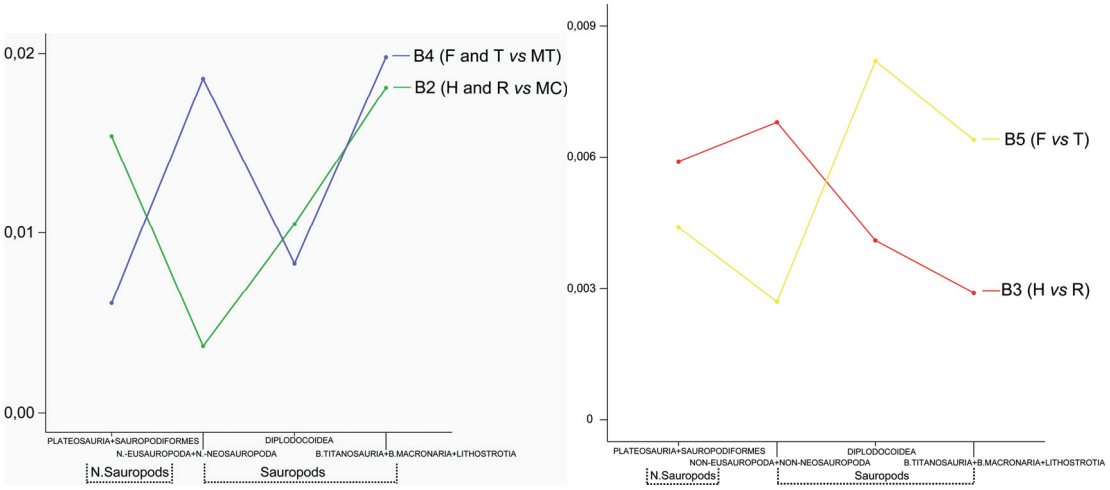

Figure 6.17 a) variance decomposition plot for balances of homologous parts B2 and B4. b) variance decomposition plot for balances of homologous parts B3 and B5.

Groups

One detects that the group showing most variability between limbs, balance B1, is non-sauropods (58%), followed by basal sauropods (23.8%) and derived sauropods (17.1%). This seems to reflect that non-sauropods present low morphological integration between limbs due to its high variability. On the contrary, derived sauropods exhibit higher morphological integration between limbs, since it present lower variability.

In terms of groups balances, non-sauropods show the biggest variance of all groups (34.7% of total variance), followed by Macronaria (27.7%), non-Eusauropoda and non-Neosauropoda (22.9%) and Diplodocoidea (14.7 %). This means that, in the analyzed groups, non-sauropods show the largest variability within individuals and Diplodocoidea exhibit the least variability among individuals. Plateosauria and Sauropodiformes exhibit most of the total variance on B1 (balance between limbs), a fact responsible for its major group variance, since on other balances this group does not reveal any major variance.

The group that shows the biggest variance in at least two balances – B2 and B4 – is Macronaria, that is to say, derived sauropods. These two balances are

anatomically equivalent, since they refer to stylopodium and zeugopodium vs. autopodium of both limbs. Therefore, Macronaria show more variability when one considers the proportions of the three limb elements altogether.

Diplodocoidea exhibits the highest variance among groups in B5. Thus, diplodocoids present the larger variability among individuals for hind limb proximal parts - femur vs. tibia, followed by the Macronaria. The least variable group in this balance is basal sauropods. Considering the balance – B3 - of the homologous elements in fore limb – humerus vs. radius, basal sauropods is the group that displays the larger variability among individuals.

The observed B3 biggest variability in proportions among individuals and the smallest variability in B5 reveal a probable condition for the basal sauropods: non-Eusauropoda and non-Neosauropoda are more conservative regarding hind limb proximal parts proportions, than the proportions of equivalent parts in the fore limb. This difference between stylopodium and zeugopodium parts of fore (higher variability) and hind (lower variability) limbs is also observable in non-sauropods, like Plateosauria and Sauropodiformes. The other sauropod groups, that is to say, derived sauropods, exhibit more variability in the proximal elements of the hind limb than in the homologous components of the fore limb.

The trend in B3 is a reduction in the variability among individuals along the sauropod clade, while in B2 - humerus and radius vs. metacarpal – the trend is the opposite, the variability among individuals increasing along the sauropod clade, namely derived sauropods.

Concerning the balances analyses illustrated in figure 6.17 and the table of the decomposition of the variance, one notices, studying balance 1 (B1), between fore and hind limb, that the biggest variability (0.0434) is observed in Plateosauria and Sauropodiformes, whereas the smallest variance between the two limbs could be quantified on Diplodocoidea (0.0008). B1 is the only balance in which Prosauropoda

reveal the major variance, although in B2 the variance (0.0154) is similar to that of derived sauropods, that is to say, basal Titanosauria, basal Macronaria and Lithostrotia (0.0181).

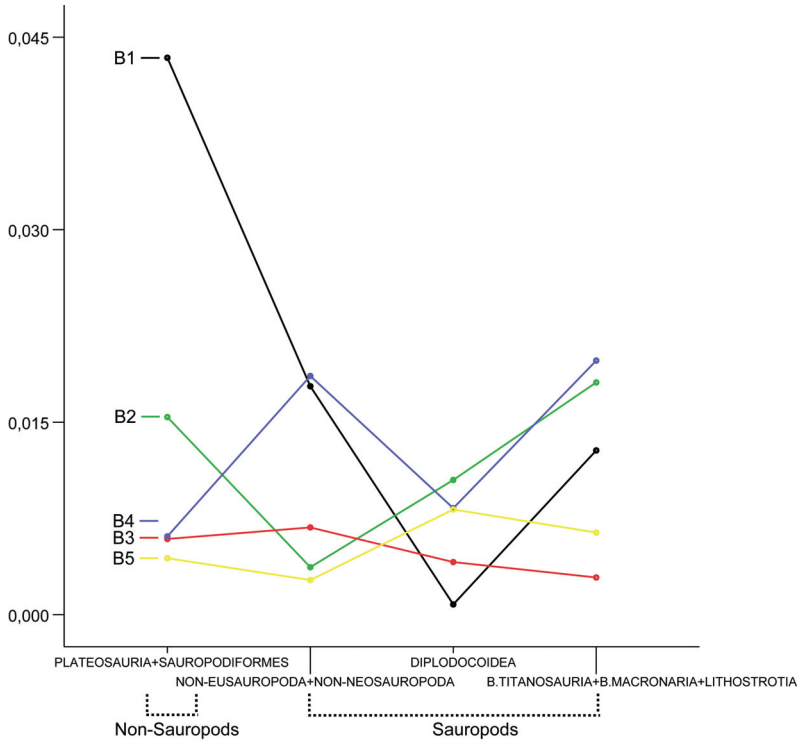

Figure 6.18 Variance decomposition plot for all balances for the different sauropodomorphs.

The fact that prosauropods exhibit the biggest variance in the balance that separates fore from hind limb elements could be interpreted by the fact that full quadrupedal animals are more conservative in limb proportions/variability than bipedal or facultative quadrupedal animals. The bipedal/facultative quadrupedal group Plateosauria and Sauropodiformes, exhibits, therefore, more variability when one deals with fore vs. hind limb elements. Corroborating this discrepancy among fore vs. hind limb variability, one verifies that bipedal dinosaurs, as theropods, exhibit the highest B1 variance among all groups in the sample - see chapter 7.

Balances centers

The centers of the segments representing the variances for each group in B1 allows as statement that the geometric mean of the parts femur, tibia and metatarsal III is greater than the geometric mean of the parts humerus, radius and metatarsal III for non-sauropods - figure 6.16. This balance could be, in future studies, employed to better discriminate prosauropods from sauropods. Balance B4 also permits to separate prosauropods from sauropods, since there is no overlapping in groups geometric centers. This fact could be detected by the clear separation of sample centers of the referred two groups, in which sauropods are placed more to the left than the sample center of Plateosauria and Sauropodiformes – figure 6.16. The balance of femur and tibia vs. metatarsal III could be a quantitative indicator of a sauropod condition, that is to say, could be employed in a Discriminant Analysis study.

The traditional attribution of bipedality in prosauropods vs. quadrupedality in sauropods would have led us to think primarily in the fore limb parts balances (B2 or B3), as being more informative on the dual locomotor condition of Sauropodomorpha. Instead, one has verified that balance B4, which deals with hind limb parts, is one of the most informative on the sauropod condition.

6.9 Final remarks

A pattern of variations in limb proportions copes with a number of biological issues, as the modular construction of limbs and their degree of variation, the relevance of size in relative proportions, the meaning of the proportions in term of its functional significance or the meaning of pattern variations in proportion and its morphological variation. These questions should be accurately prospected in future works, although a few preliminary statements can be here addressed, according to the obtained results.

Modular structures such as limbs or axial column deal with a chain of elements. Variation among modular elements has been classically located at their distal most elements, because these were not so constrained as the remainders and also due to developmental factors that accumulate variation in distal parts[‡‡]. For example, based on Table 6.11 and considering the sample with the six elements preserved, it may be posed that there is a gradient in the variation of limbs, so that distal elements show more variability than proximal ones. That occurs clearly for Sauropoda fore and hind limbs, although the trend has some exceptions in Prosauropoda, since the general trend is not observed in metacarpal. As for the prosauropod hind limb, femora is slightly more variable than tibia.

1) Through the distinct and varied compositional data analyses herein performed on the appendicular skeleton parts, it has been established that sauropodomorphs could be divided into two distinct limb proportions groups: 'Prosauropoda' and derived sauropods, such as basal Macronaria, basal Lithostrotia and Lithostrotia. The taxa phylogenetically positioned in between the above cited groups present transitional forms in terms of proportions.

The appendicular skeleton relationships of size and disparity show dissimilar trends within sauropods. The fore limb of basal sauropods (i.e., non-eusauropods and non-neosauropods) reveals an opposite relationship of size and limb proportions disparity when compared to derived sauropods (i.e., diplodocoids and macronarians), since the larger basal most sauropods present higher disparity indexes, while derived sauropods show an opposite relation of disparity and size. Two patterns of sauropods fore limb morphospace occupation could, therefore, be defined: one for basal sauropods and another for derived sauropods.

[‡‡] "Hallgrímsson et al. (2002) demonstrated in macaques that phenotypic and environmental variances increase and heritability decreases as one moves down the limb. These results are predicted by the fact that development proceeds proximodistally, thus variation will tend to accumulate in distal structures." Young and Hallgrímsson 2005, p.2701.

Regarding the hind limb, the most primitive (non-eusauropods) and derived (lithostrotians) sauropods show identical behavior in the proportions morphospace, that is to say, bigger individuals correspond to smaller disparity indexes. Oppositely, all the remaining sauropod groups reveal that bigger individuals have higher disparity indexes. Consequently, sauropods seem to have explored the hind limb morphospace more extensively as they were increasing in size.

2) The group Prosauropoda revealed distinct relationships of size and disparity, among its groups, since all bone parts, except the metacarpal in Plateosauria and Sauropodiformes, show opposite trends in morphospace occupation: Plateosauria bigger individuals are more conservative, that is, show smaller disparity indices, while Sauropodiformes bigger individuals reveal higher disparity indices. Thus, in what concerns size, prosauropods do not present a homogeneous positioning in the morphospace.

3) The analyses performed took into account the existence of non-adults in the sample and the results revealed that, when one removes those specimens, the previously identified relationships of size and disparity are significantly changed in most of the groups. Therefore, there are two patterns of sauropods morphospace construction: one for adults and a distinct one for non-adults, implying a probable existence of appendicular heterochrony in sauropods.

4) The balances analyses allowed identifying bone elements which proportions discriminate sauropodomorphs groups. The balance of fore limb parts vs. hind limb parts was read as informative on the prosauropod or sauropod nature of the specimen, as well as on the degree of morphological integration between limbs.

Additionally, the balance of hind limb parts, femur and tibia vs. metatarsal, also revealed itself as an important source of information in order to discriminate prosauropods and sauropods. Previously, this balance was not considered as informative as the fore vs. hind limb in this discriminative context. Thus, the role of the

hind limb proportions should be analyzed in detail in further studies, since it was herein identified as an essential factor in the appendicular proportions differences among prosauropods and sauropods. The two modes of locomotion among these groups could be more deeply linked to the hind limb proportions than was previously thought.

It can be declared as a fact that Sauropodomorpha locomotion evolutionary history is more complex than the mere bipedal-quadrupedal categorization - see chapter 7. The important role of the hind limb in the sauropodomorph locomotor specializations have only been associated with femur morphological differences among sauropods, namely Titanosauria (Wilson and Carrano 1998), but not with bone parts proportions. It has been referred that morpholological differences among the sauropodomorphs ichnological record are linked mainly with the hind limb digits rotation (Rodrigues and Santos 2003).

Concerning the fore limb, it was identified that, in derived sauropods, size and disparity are inversely related. Also, derived sauropods present generally bigger sizes than primitive sauropods. It could therefore be speculated that size is, in this group, a constraining factor of proportions disparity and that the role of the fore limb in derived sauropods is a mere supportive structure. The enlarged supportive function of the fore limb is, as well, morphologically reflected on the reduction or loss of phalanx that some sauropod taxa.

Although the fore limb proportions remain conservative among derived sauropods, it should be noted that the relative proportion of fore limb vs. hind limb is distinct in some taxa, like basal macronarians. The increase of the fore limb comparatively to the hind limb is justified by some authors as an additional morphological argument for different niche exploration, that is to say, additionally to the neck size increase, the relative lengthening of the fore limb contributed to a distinct feeding strategy among basal macronarians - high-browsing - while, for example,

diplodocoids were considered as low-browsing sauropods (e.g., Bakker 1987; Paul 1987, 1988; Barrett and Upchurch 2007).

5) the study of variation of fore limb and hind limb bone proportions allowed to identify that differences between non-sauropods and sauropods are more reflected in the hind limb than in the fore limb. This fact implies that typical bipedal- or quadrupedal-type locomotion in sauropodomorphs is far more complex than the mere analysis of the fore vs. hind limb ratio study allows. This important question is complemented in the following chapter. As seen above, one has verified that balance B4, which deals with hind limb parts, is one of the most informative on the sauropod condition.

7 – Dinosauria and Mammalia Limb Disparity and Morphospaces

"The point about explanation in biology that I would particularly like to stress is this: to understand organisms one must explain their organization. It is elementary that one must know what is organized and how it is organized, but that does not explain the fact or the nature of the organization itself. Such explanation requires knowledge of how an organism came to be organized and what function the organization serves.

Ultimate explanation in biology is therefore necessarily evolutionary."

Simpson, George Gaylord, *This View of Life: The World of an Evolutionist,* p. 113

This chapter will be centered, similarly to chapter 6, on the variability of both limbs proportions among distinct groups of tetrapods. However, the sample used in this chapter is a wider one and integrates mammals, birds, crocodiles and distinct groups of dinosaurs, such as theropods, ornithischians or sauropodomorphs.

All of the following analyses adopted methodological procedures as the ones used in chapters 3 and 6, namely in the exploration of morphospace occupation patterns, the quantification of disparity within and among groups (intra- and interdistances), the analyses of biplots and balances, and the performing of statistical tests.

7.1 MATERIALS

Various dinosaur and dinosaur related groups – Dinosauromorpha, Theropoda, Aves and Ornithopoda – as well as non-dinosaur groups - Mammalia and Crocodylia - are used as comparison components and will be confronted within each limb morphospace, in order to evaluate the occupation and disparity patterns of sauropodomorphs and identify patterns of limb proportions variability. The application of this methodological framework will provide an opportunity to explore the versatile organization of quadrupedia in Sauropodomorpha in relation to other quadrupeds in Dinosauria or in mammals.

Theropoda were divided in 4 groups: Basal; Ceratosauria (Marsh, 1884b); Coelurosauria (Huene, 1914); Theropoda – Carnosauria (Huene, 1920). Due to the reduced number of specimens with three complete segments, the Aves forelimb sample was selected from the Dyke et al. 2006 database. 20 bird specimens, 10 Passerines and 10 Non-Passerines were randomly selected. The Aves hind limb sample is from Middeleton and Gatesy (2000). The sample of Ornithopoda dinosaurs was divided into two sub-groups: non-Iguanodontia and Iguanodontia. In terms of locomotion, one should state that quadrupedality among iguanodontians is supported

by the presence of numerous adaptations for weight-bearing in the carpus and manus (Norman 1980), as well as by ichnological evidences (Norman 1980; Moratalla et al. 1992, 1994b; Pérez-Lorente et al. 1997).

All dinosaur specimens are grouped as described, but in some analyses, due mainly to sample size, some of the groups were, by option, aggregated. The criteria used are identified along the analyses.

The Mammalia sample was divided into Prototheria, Metatheria and Eutheria. Given the large number of Eutheria specimens, the option prevailed to divide them into Perissodactyla and Artiodactyla. Mammal limbs are adapted for different forms of locomotion, but the criteria was to select mammals that could be used as functional equivalents to the majority of sauropodomorphs, namely Artiodactyla and Perissodactyla. Limb elements lengths of derived as well as of primitive mammal groups were compiled in order to control a possible phylogenetic signal within this group.

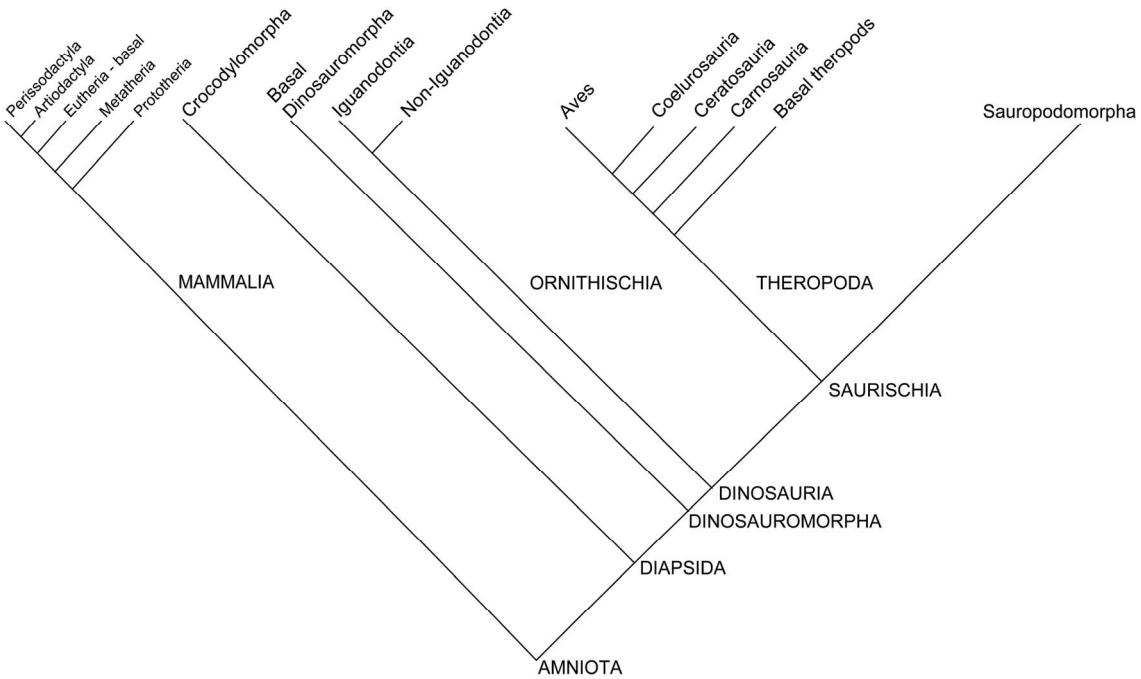

Figure 7.1 Simplified phylogenetic relationships of the Amniota groups used in the current analysis.

7.2 Limb Morphospaces

In the fore limb morphospace two domains could be identified, despite the partial overlapping of certain groups:

a) one domain is occupied by individuals with femur proportions ranging from around 30 to 50%, the metatarsal proportions ranging from around 17 to 40% and tibia proportions fluctuating around 40%. The groups that occupy this morphospace domain are mostly Perissodactyla, Artiodactyla, Iguanodontia, Passerines and non-Passerines;

b) the other domain comprises specimens with femur proportions ranging from 40 to 60%, metarsal proportions of less than 17% and tibia proportions varying from 30 to 50%. Individuals that fulfill this morphospace domain belong typically to Sauropoda, Prosauropoda, Theropoda and Metatheria.

In the hind limb morphospace, three domains could be identified, despite some specimens overlapping:

a) one domain is filled with specimens with femur proportions lower than 40% and metatarsal proportions ranging from around 22 to 35%. This domain is occupied mainly by individuals belonging to Artiodactyla, the majority of Theropoda, Aves and non-Iguanodontia;

b) an intermediate domain represents individuals with femur proportions from 40 to around 50% and metatarsal proportions between 17 to 22%. Specimens located in this morphospace domain belong mainly to Iguanodontia, Carnosauria, Plateosauria and Sauropodiformes;

c) one domain includes individuals with femur proportions around or higher than 50% and metatarsal proportions of less than 17%. The animals placed in this domain belong mainly to Perissodactyla and Sauropoda.

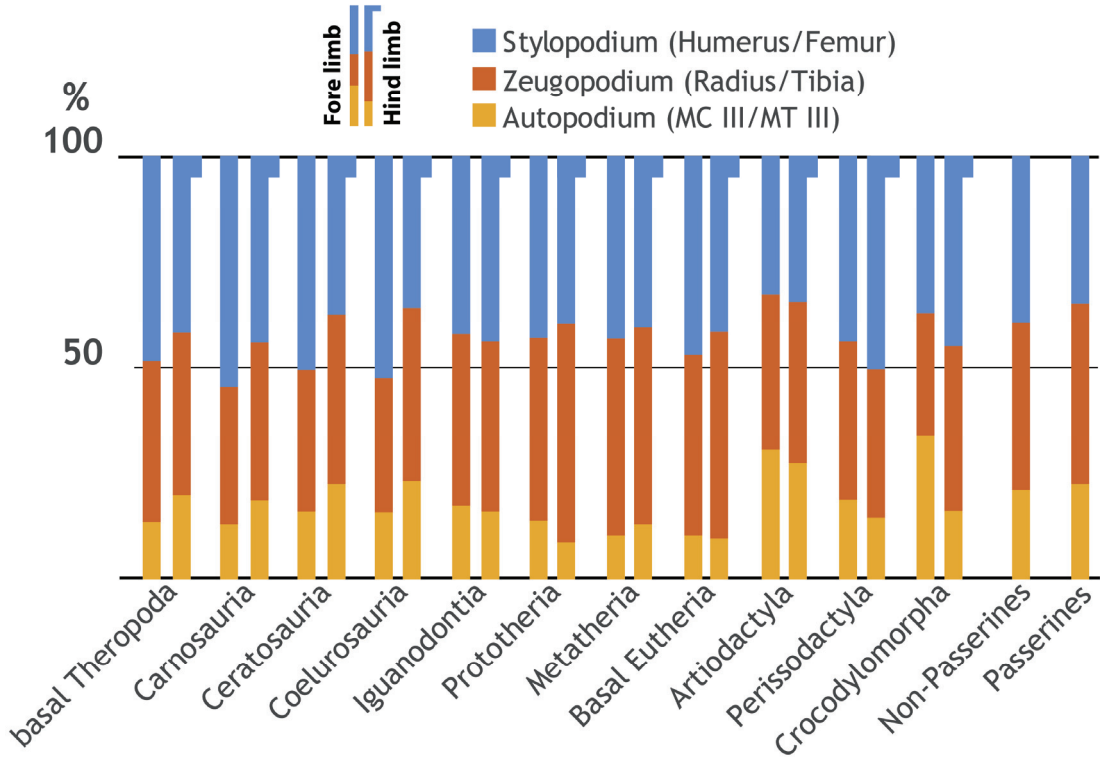

Figure 7.2 Fore and hind limb proportions centroids of different Amniota groups. For both Aves groups - Passerines and non-Passerines, only fore limb proportions is depicted.

Regarding the fore limb extreme forms, one notices that sauropodomorphs and most of the theropods could be included in this category. Closer to fore limb extreme forms are the non-Iguanodontia, as well as basal theropods, showing humerus proportions nearer to 50%. All other groups analyzed present less than half of the percentage in the humerus proportion and could not be considered as stylopodium extreme forms.

The hind limb extreme proportions offer us a different reality, since sauropodomorphs and Perissodactyla reveal more than 50% of the total length of the three analyzed bones. These groups are located in the area of the ternary morphospace, classified as stylopodium dominated area. Oppositely to what was described regarding the fore limb, in the hind limb there are some groups that exhibit a zeugopodium length with more than 50% of the total length, namely, the tibia

proportion prevails upon the other bones. Examples of stylopodium dominated hind limb are the Prototheria and, close to this group, the basal Eutheria.

Among the analyzed groups, none was identified that presented autopodium dominated limbs. The only species close to this definition, and only in the hind limb, is the artiodactyl *Giraffa camelopardalis*.

7.2.1 Mammalia

The high importance of the zeugopodium in Metatheria is noticeable due to the relative length of the radius, that is to say, the intermediate part shows the length preponderance in fore limb proportions. Therefore, metatherians are near the definition of zeugopodium dominated fore limbs. In the hind limb, it is also the zeugopodium bone, the tibia, which shows the higher proportion in the limb, but with a higher divergence to the proximal bone than was observed in the fore limb.

Artiodactyla is, among all analyzed groups, the one that reveals the more homogeneous distribution of bone proportions, both in fore and hind limbs. Artiodactyls present the intermediate bone limb as the most important in both limbs - radius and tibia, but the proximal and distal bones show closer proportions, fact more evident in the fore limb.

Perissodactyls fore limb shows a stronger influence of the humerus in limb proportions and, in the hind limb, Perissodactyla could be included in the definition of stylopodium dominated limb, due to the high percentage of the femur - 50.38%.

Clearly perissodactyls and artiodactyls morphospace centroids are distinguishable by the bone that shows the higher proportion: artiodactyls present the intermediate bone as the most important, radius and tibia, while perissodactyls proximal bone, humerus and femur, is the part with higher proportion in both limbs.

Artiodactyls and perissodactyls occupy two distinct sub-areas of the fore limb morphospace, although both groups are integrated in the above cited domain.

Artiodactyla individuals are located in an area corresponding to lower humerus proportion and higher metacarpal relative length. The majority of these mammals lie on the most extreme area of the total fore limb morphospace, being the most extreme in the autopodial proportion.

Despite the identifiable separation between Artiodactyla and Perissodactyla, there seems to be a continuity of occupation of the morphospace of these two groups.

In the hind limb morphospace there is, once again, a gap between Perissodactyla and Artiodactyla, although much more evident than in the fore limb. That is to say, the two mammal groups are more distinguishable in the hind limb morphospace than in the fore limb morphospace. In the hind limb morphospace, most of perissodactyls occupy a similar morphospace area to sauropods, while artiodactyls are separated in an area corresponding to higher metatarsal proportion. Closer to artiodactyls are the non-ornithopods, ceratosaurs and coelurosaurs. The former two groups of theropods are bipedal animals and this fact in intriguing and should be analyzed in detail in future studies.

Non-eutherian mammals (Prototheria and Metatheria) occupy a specific area of the fore limb morphospace, well classified by the higher radius proportion. In the hind limb morphospace, Prototheria and Metatheria lie in a specific domain which, similarly to the fore limb, is distinguishable by the higher proportion of the zeugopodial bone (tibia). Clearly, metatherians occupy a sub-area, both in fore and hind limb morphospaces.

Centroids	Fore limb				Hind limb			
	n	H	R	MC	n	F	T	MT
Dinosauromorpha	1	40.00	25.71	34.29	7	37.74	41.58	20.68
Theropoda	(11)	51.61	33.11	15.28	(109)	37.55	40.13	22.32
Basal	2	48.34	38.08	13.58	6	41.84	38.16	20.00
Carnosauria	1	54.49	32.40	13.11	16	44.08	37.19	18.73
Ceratosauria	2	50.59	33.32	16.09	19	37.34	40.05	22.61
Coelurosauria	6	52.46	31.55	15.99	68	35.76	40.92	23.32
Basal sauropodomorphs+Plateosauria+Sauropodiformes	(10)	56.39	32.10	11.51	(34)	44.45	37.52	18.03
Basal Sauropodomorphs	0	[3]	[3]	[3]	3	42.00	37.53	20.47
Plateosauria	5	56.04	31.22	12.74	22	44.78	37.57	17.65
Sauropodiformes	5	56.65	32.96	10.39	9	44.45	37.36	18.19
Non-Eusauropoda+ Non-Neosauropoda	(9)	50.93	35.80	13.27	(12)	54.88	34.62	10.50
Non-Eusauropoda	1	45.07	41.65	13.26	4	53.00	35.24	11.76
Non-Neosauropoda	8	51.65	35.09	13.26	8	55.79	34.28	9.93
Diplodocoidea	7	51.51	34.62	13.85	6	55.97	35.05	8.98
Basal Macronaria+Basal Titanosauria+Lithostrotia	(14)	51.40	32.49	16.11	(17)	56.64	33.99	9.37
Basal Macronaria	6	51.47	33.28	15.25	8	56.17	35.94	7.89
Basal Titanosauria	2	50.68	31.76	17.56	3	54.95	36.01	9.04
Lithostrotia	6	51.54	31.95	16.51	6	55.97	35.05	8.98
Ornithopoda - Iguanodontia+Non-Iguanodontia	(12)	42.85	40.37	16.78	(29)	40.56	40.99	18.45
Iguanodontia	11	42.19	40.25	17.56	15	43.84	40.12	16.04
Non-Iguanodontia	1	49.48	40.63	9.90	14	37.07	41.65	21.28
Prototheria	1	43.01	43.01	13.98	3	39.61	51.41	8.98
Metatheria	31	43.21	46.30	10.49	16	40.62	46.33	13.05
Basal Eutheria	2	47.01	42.44	10.55	1	41.64	48.63	9.73
Artiodactyla	64	32.76	36.68	30.56	66	34.51	38.05	27.44
Perissodactyla	24	43.93	37.22	18.85	33	50.38	34.99	14.63
Crocodylomorpha	1	37.10	28.76	34.14	2	44.92	38.88	16.20
Aves – Passerines+Non-Passerines	(20)	37.08	41.00	21.92	(18)	34.50[1]	44.02[1]	21.48[1]
Non-Passerines	10	39.46[2]	39.31[2]	21.23[2]	[2]	[2]	[2]	[2]
Passerines	10	34.76[2]	42.66[2]	22.58[2]	[2]	[2]	[2]	[2]

Table 7.1 Fore limb centroids for H – humerus; R/U – radius; MCIII – metacarpal III. 1 – the Aves specimens used for the hind limb are all fossil; 2 – fore limb data taken randomly from Dyke et al. 2006 sample; no hind limb data – section 3.2; 3 - there are no basal sauropodomorphs with three fore limb bones preserved. Abbreviations: F – femur; H – humerus; MC – metacarpal III; MT – metatarsal III; R – radius; T – tibia.

7.2.2 Theropoda

Concerning group centroids, one detects that Carnosauria, Ceratosauria and Coelurosauria are stylopodium dominated fore limbs, that is to say, the humerus represents more than 50% of the fore limb length, with 54.49, 50.59 and 52.46 per cent, respectively. Similarly to what was detected in almost all sauropodomorphs, theropods analyzed herein reveal a dominant bone, that is, a bone part which clearly dominates the total relative limb length, namely the proximal limb bone.

Theropods reveal a conservative zeugopodium relative length, the radius, being the most distal bone, the metacarpal, the element that shows Centroids variability.

Theropods hind limb does not reveal extreme proportions similar to fore limb, since there is not a majority proportion of any bone. Unlike the fore limb, the intermediate limb bone, the tibia, is the element that shows the higher proportion in most derived theropod groups - Ceratosauria and Coelurosauria, with approximately 40 and 41 %, respectively. The main differences in Theropods hind limb are focused, therefore, in the two most proximal bones femur and tibia, and one can detect a change in proportion dominance within Theropods: the most primitive reveal higher percentage of femur, while the derived, as stated, show bigger tibia differences. Despite this, one should also state that theropod metatarsal group centroids range from 18 to 23%.

Figure 7.3 (fore limb morphospace) permits detecting that theropods, sauropods and prosauropods are very closer, occupying a restrict area of the morphospace and well separated from the mammals. This fact allows speculating about the existence of a well marked saurischian fore limb morphospace domain.

In the hind limb morphospace, the differences among the Saurischia groups are more pronounced than in the fore limb, since prosauropods and theropods lie in an intermediate morphospace area between artiodactyls and the sauropods and perissodactyls.

The fore limb morphospace of theropods is somewhat disperse and there is no clear trend of occupation. Theropods occupy closer areas to sauropods than to prosauropods, which are the most extreme specimens in the fore limb morphospace.

Theropods hind limb morphospace is compact and sort of rounded in shape, thus revealing an homogeneous exploration of all the bone proportions. The only group that reveals a linear trend, changes in femur and tibia proportions, is the Carnosauria.

All Theropods, except coelurosaurs, are positioned, as stated above, in an intermediate area in the hind limb morphospace, between sauropods, and perissodactyls and artiodactyls.

7.2.3 Ornithischia

Since non-iguanodontids sample is constituted by only one specimen, the focus will be given to Iguanodontia centroids only. Iguandonontia shows sub-equivalent percentages of the two most proximal bones, humerus and radius, with approximately 42 and 40 %, respectively.

Ornithsichians hind limbs are distinguishable mainly by differences in the most distant bone parts proportions, that is, femur and metatarsal; the intermediate bone reveals approximately equivalent proportions in both groups. Non-iguanodontids femur exhibits a smaller proportion than iguanodontids, originating that the tibia of the former group has most of the relative length of the limb.

Both ornithsichian groups are well separated in the hind limb morphospace, iguanodontids occupying closer areas to Carnosauria and Perissodactyla. This fact is intriguing, since those carnosaurs and perissodactyls represent two modes of locomotion - bipedality and quadrupedality, respectively.

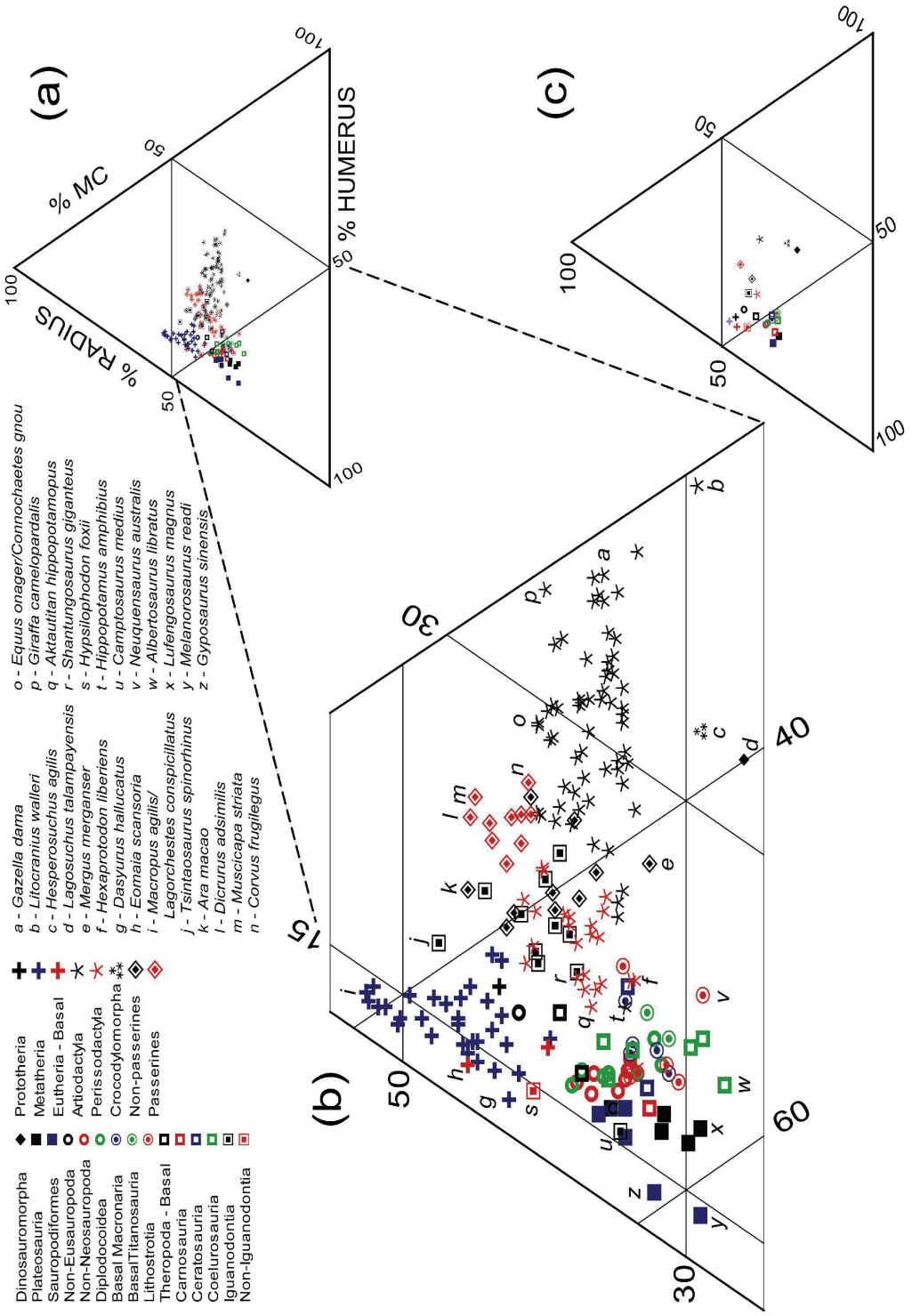

Figure 7.3 a) Fore limb elements morphospace of different Amniota groups; b) occupied area of morphospace; some specimens in the morphospace outskirt are identified; c) ternary diagram of groups centroids. Abbreviations: % H – humerus percentage; % MC – metacarpal III percentage; % R – radius percentage.

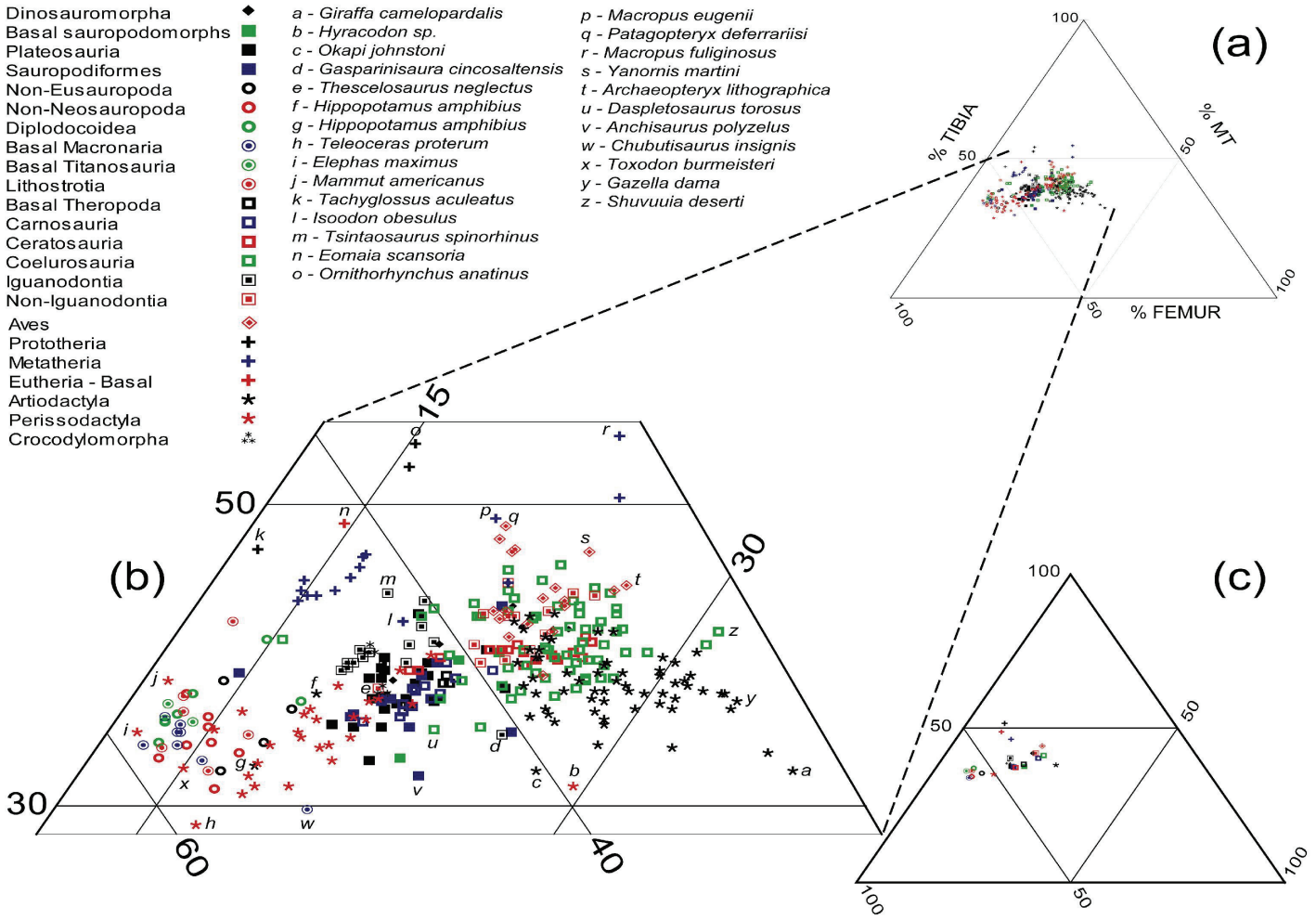

Figure 7.4 a) Hind limb elements morphospace of different vertebrate groups; b) occupied area of morphospace; specimens in the morphospace outskirt are identified. c) Morphospace of group centroids. Abbreviations: % F – femur percentage; % MT – metacarpal III percentage; % T – tibia percentage.

Final remarks

The analyses of both limbs morphospaces, as well as the group centroids, allowed to identify patterns of occupation within the ternary diagrams - figures 7.3 and 7.4, table 7.2.

Interesting is the fact that the considered typical bipedals (e.g., theropods) are more distinguishable when compared to quadrupedals (e.g., sauropods) in the hind limb morphospace than in the fore limb morphospace. In other words, in the hind limb morphospace there is a more evident gap area between the two modes of locomotion than in the fore limb morphospace.

A saurischian area has been detected within the fore limb morphospace. A similar tendency of Saurischia groups has not been verified in the hind limb morphospace.

On should also mention that the intermediate bone of the hind limb is the most stable element, that is to say, the tibia proportion does not allow to clearly discriminate the majority of the groups within the above cited hind limb morphospace domains. The equivalent fore limb intermediate bone, the radius, only allows discrimination within one of the domains - between the Metatheria and Saurischia groups.

7.3 Morphospace fringe specimens

Concerning the fore limb of all specimens, one can identify some specimens in the outskirt of the ternary morphospace. *Mergus merganser* (diver/swimmer, Zeffer et al. 2003) and *Ara macao* (arboreal, Zeffer et al. 2003) are two of those cases, in the non-Passerines sample. Among the Passerines sample, *Corvus frugilegus* (ground, Zeffer et al. 2003), *Dicrurus adsimilis* and *Muscicapa striata* are well identified on the border of its morphospace region.

Comparing this morphospace visual identification to intragroups A.D. outliers - figures 7.5, it is noticeable that both Passerines and non-Passerines do not present any deviant element, oppositely to what could be identified by the “visual-only” approach.

Regarding the Dinosauromorpha and Crocodylomorpha relative positioning in the morphospace, as well as its reduced sample size, it would be desirable for future studies to focus on these groups, particularly on the latter one, since there should be available extant specimens.

As for artiodactyls, *Litocranius walleri* and *Gazella dama* reveal the longer autopodium, which is associated with a reduced humerus. It has been referred that the long limbs of these animals are an adaptation to feeding on the high level browse (Scott 1985). *Giraffa camelopardus* is an easily recognizable artiodactyl in the morphospace, but differs from *L. walleri* and *G. dama* by its proportionally smaller MC III and bigger radius. On the other extreme, namely artiodactyls with proportionally longer humerus and smaller MC III, is *Hippopotamus amphibious*.

7.4 Intragroups A.D.

The intragroups A.D. were computed for the diverse groups and for each limb - table 7.2.

7.4.1 Mammalia

Mammals intragroups A.D. reveal that the most conservative group in the fore limb is Perissodactyla, as it has the smallest SD, followed by Metatheria and Artiodactyla. One could detect that the conservative pattern of perissodactyls fore limb is not maintained regarding the hind limb, due to its high disparity values - A.D. of 0.215 and SD of 0.188. The less disparate mammal group in the hind limb is Artiodactyla, occupying a more confined morphospace area than other mammals.

Intragroups A.D.	Fore limb				Hind limb			
	n	Me.	Mx.	SD	n	Me.	Mx.	S.D.
Dinosauromorpha	1	**	**	**	7	.125	.076	.251
Theropoda – Basal+Carnos.+Cerato.+Coeluro.	11	.163	.243	.070	109	.171	.104	.750
Basal	2	.091	.091	.000	6	.037	.096	.033
Carnosauria	1	**	**	**	16	.070	.183	.049
Ceratosauria	2	.144	.144	.000	19	.102	.277	.078
Coelurosauria	6	.155	.222	.049	68	.155	.809	.115
Ornithopoda – Iguanodontia+Non-Iguanodontia	12	.208	.502	.161	29	.196	.361	.081
Iguanodontia	11	.171	.526	.144	15	.114	.429	.094
Non-Iguanodontia	1	**	**	**	14	.111	.319	.073
Basal sauropodomorphs+Plateosauria+Sauropodiformes	(10)	.140	.232	.058	(34)	.127	.589	.112
Basal Sauropodomorphs	0	1	1	1	3	.117	.167	.048
Plateosauria	5	.079	.152	.053	22	.088	.277	.059
Sauropodiformes	5	.125	.172	.049	9	.198	.597	.179
Non-Eusauropoda+ Non-Neosauropoda	(9)	.099	.194	.047	(12)	.152	.285	.076
Non-Eusauropoda	1	**	**	**	4	.146	.249	.069
Non-Neosauropoda	8	.082	.127	.036	8	.124	.244	.086
Diplodocoidea	7	.119	.197	.065	6	.172	.377	.103
Basal Macronaria+Basal Titanosauria+Lithostrotia	(14)	.120	.309	.086	(17)	.163	.631	.146
Basal Macronaria	6	.101	.254	.087	8	.181	.586	.175
Basal Titanosauria	2	.035	.035	.000	3	.118	.162	.042
Lithostrotia	6	.147	.246	.071	6	.181	.259	.078
Prototheria	1	**	**	**	3	.240	.358	.103
Metatheria	31	.155	.356	.085	16	.267	.645	.172
Basal Eutheria	2	.171	.171	.000	1	**	**	**
Artiodactyla	64	.188	.679	.124	66	.173	.826	.139
Perissodactyla	24	.122	.304	.060	33	.215	.757	.188
Crocodylomorpha	1	**	**	**	2	.067	.067	.000
Aves – Passerines+Non-Passerines	20	.143	.306	.066	18	.123	.215	.059
Non-Passerines	10	.156	.271	.079				
Passerines	10	.072	.129	.032				

Table 7.2 – Fore and hind limbs intragroup Aitichinson distances (A.D.) arithmetic mean (Me.); SD - standard deviation; Mx, – maximum; ** - single specimen. 1- sub-group Basal Sauropodomorphs does not present any specimen with all three bones preserved.

7.4.2 Theropoda

Wider considerations on theropod groups fore limb disparity could not be made due to the reduced sample. Taking this into account, and reporting only to the mean intragroup A.D. and not the SD, one could observe that there seems be an increase of disparity along the Theropoda clade.

The disparity in the hind limb shows a similar reality, and a more corroborated approach, since there is an increase of both A.D. and SD along the clade Theropoda, that is to say, derived theropods reveal higher A.D. and SD than primitive theropods. It

should be also noticed that Coleurosauria reveal identical A.D. both in fore and hind limbs, but the analysis of the SD confirms a higher disparity in coelurosaur hind limb.

7.4.3 Ornithischia

The single specimen of non-Iguanodontia group invalidates the comparison of disparity among ornithischians fore limb. This approach could be performed in the hind limb, regarding which one notices that both groups show sub-identical disparity values, although Iguanodontia is slightly more disparate than non-Iguanodontia.

7.4.4 Aves

Non-Passerines exhibit more disparity in the fore limb than Passerines, the latter being less disparate when compared to Coelurosauria. Moreover, comparing the disparity results among bigger groupings, that is to say, comparing Aves (non-Passerines and Passerines) against all theropod groups, one detects that, in fore limb, theropods reveal a slightly higher disparity than Aves - A.D. of 0.163 and 0.143 and SD of 0.070 and 0.066 for both cases, respectively.

Performing a similar comparison for the hind limb, one discovers that disparity is considerable higher in theropods than in Aves. The latter group sample is constituted only by fossil specimens and, comparing the hind limb disparity of Aves and Coelurosaurs, one finds that the former group is less disparate than theropod dinosaurs.

7.5 A.D. Outliers

In the present section, each individual specimen A.D. to its group centroid was used in order to evaluate the structure of the data and test the existence of outliers (cases with interquartile range between 1.5 and 3) and extreme values (cases with more than 3 times the interquartile range) through the use of box-plots (Tukey 1977). Both fore and hind limbs A.D. box plots are represented in figures 7.5 and 7.6.

7.5.1 Fore limb

The fore limb A.D. outlier analysis allowed to identify several outliers but none extreme elements. The outilers are the following: in Sauropodiformes, the Chinese sauropodomorph *Jingshanosaurus xinwaensis* (LV003); in Iguanodontia, *Camptosaurus medius* (CM 11337); in Artiodactyla, *Hippopotamus amphibius* (UMMZ 84041); and, in Perissodactyla, the brontothere *Aktautitan hippopotamopus* (KAN N2/876). The reduced number of outliers and the inexistence of extreme specimens in the fore limb intragroups A.D. could be justified by a more conservative pattern of the fore limb proportions and, as well, by the inferior number of specimens analyzed in comparison to the hind limb sample.

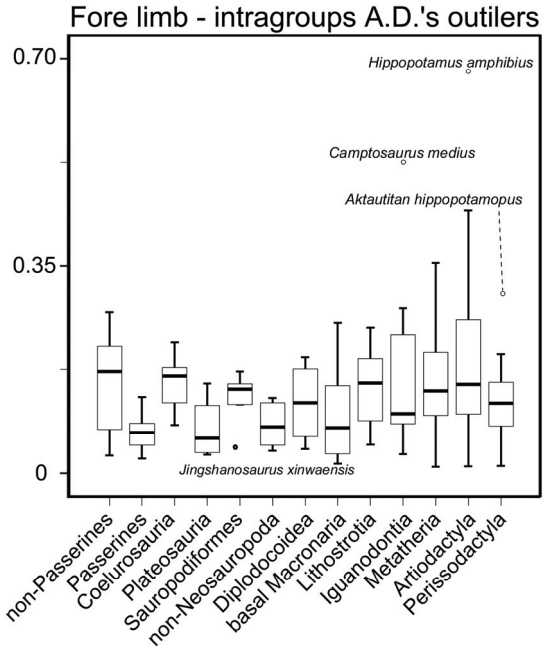

Figure 7.5 Box plot of fore limb intragroups A.D. of dinosaur and mammal groups. Outliers are represented as circles. Groups with two or less specimens are not represented.

7.5.2 Hind limb

Basal Theropoda has only one outlier, *Eoraptor lunensis* (PVSJ 512). This seems not to be related with disparity incongruence within this group, but instead with the sampling factors, since the sample has five individuals of one species - *Herrerasaurus ischigualastensis* - and only one specimen of *E. lunensis*. To

corroborate this fact, one observes that the intragroup A.D. for H. *ischigualastensis* specimens are all very similar. On the Coelurosauria sample there are four outliers: *Beipiaosaurus inexpectatus* (IVPP V11559; Holtz pers. commun.), *Parvicursor remotus* (PIN 4487/25; Holtz pers. commun.), *Velociraptor mongoliensis* (IGM 100/986; Holtz pers. commun.), *Shuvuuia deserti* (MPD 100/120; Holtz pers. commun.) and one extreme element - *Neimongosaurus yangi* (LH V0001; Holtz pers. commun.). It is interesting that four out of five of the most disparate hind limb specimens belong to two clades – Alvarezsauridae and Therizinosauroidea. Possibly, the dissimilar A.D. are due to the big number of clades included in our group Coelurosauria, as well as to limb anatomical peculiarities distinctive of the cited taxa. In future studies, a distinct selection criteria should be applied to the Theropoda group, in order to evaluate the disparity tendencies among the non-discriminated theropod dinosaurs.

Among the Iguanodontia sub-group, *Gasparinisaura cincosaltensis* (MUCPV-208; Coria and Salgado 1996) is an extreme form. In the non-Iguanodontia sub-group there is one outlier, *Leaellynasaura amicagraphica* (NMV P186047), and one extreme element, *Thescelosaurus neglectus* (NMC 8537), both hypsilophodontids.

In the Artiodactyla sample there are two extreme specimens, both *Hippopotamus amphibious* (UMMZ 84041 and FMNH 127871) and one outlier, *Giraffa camelopardis* (Lilje, pers. commun.), but they differ from the cited extreme artiodactyls since the main appendicular element is the zeugopodium.

Among Perissodactyla there are three outliers: *Elephas maximus* (FMNH 6060), *Hyracodon sp.* (YPM-PU non-numbered, Holtz 1994) and *Mammut americanus* (AMNH non-numbered, Carrano 1998a). Metatheria group A.D. reveals two outliers, both belonging to the genus Macropus: *M. fuliginosus* (FMNH 44295) and *M. giganteus* (FMNH 60153), the western and eastern gray kangaroos, respectively.

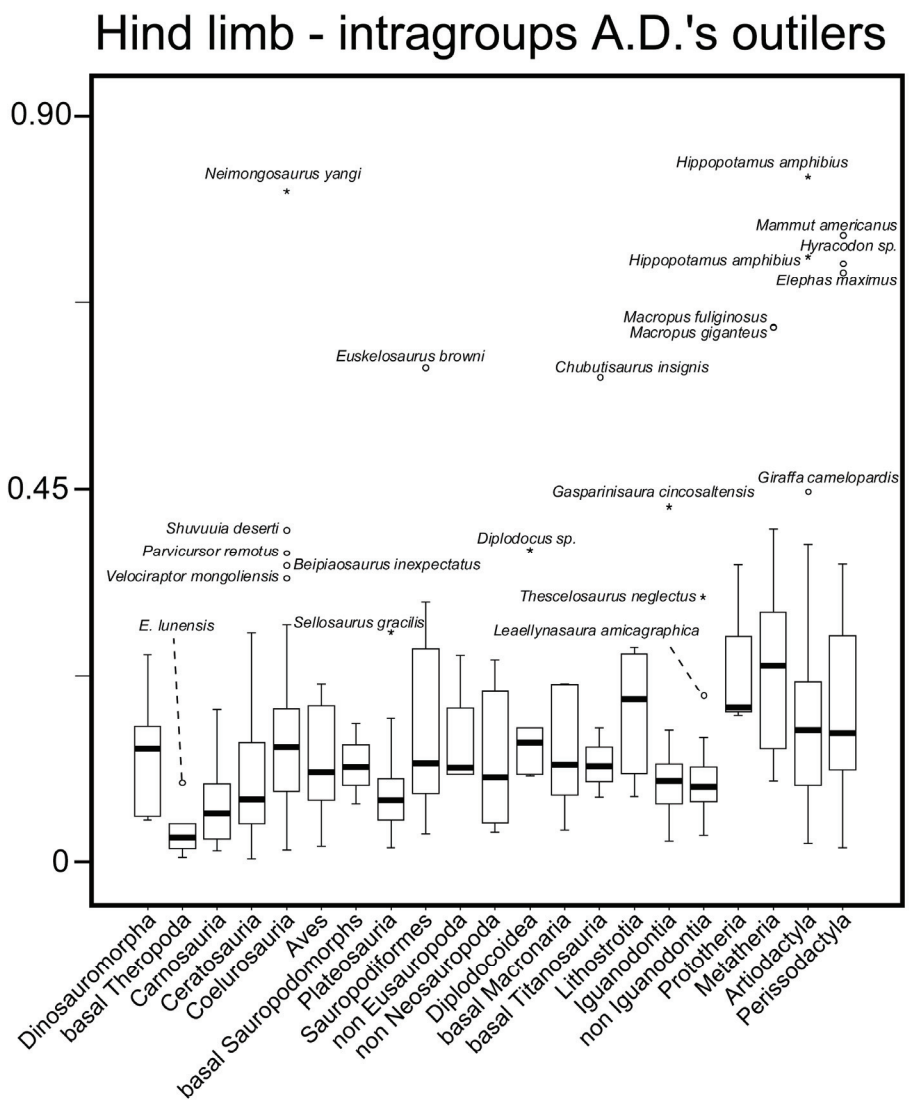

Figure 7.6 Box plot displaying hind limb intragroups A.D. of mammals. Outliers are represented as circles. Extreme forms are represented as stars. Groups with two or less specimens are not represented.

7.6 Intergroups A.D.

In the present section the intergroups A.D. were calculated for both limbs - tables 7.3 and 7.4. These A.D. permit to compare the interval between two group centroids within the proportions morphospace. In section 7.2, the location of the different groups was identified and characterized. The A.D. now offers a numeric index of the distance between the groups.

It is not the purpose of this section to make an exhaustive analysis of all the A.D. results but, instead, to identify some morphospaces distances that could

contribute to a better understanding of the morphological domains occupied by the different groups of animals.

7.6.1 Fore limb

Theropoda

Complementary to the A.D. analyses of Sauropodomorpha performed in chapter 6, one detects, in the present section, that most of the theropod groups reveal small A.D. to distinct sauropod groups, ranging from 0.035, between Lithostrotia and Coelurosauria, to 0.366 between non-Eusauropoda and Coelurosauria. Carnosauria disclose the minimal morphospace distance to Plateosauria - 0.050. These results implicate a morphological proximity between theropods and sauropodomorphs in the fore limb, which is also the reflection of the phylogenetic proximity of those groups.

A general trend in the A.D. of Theropoda and Sauropoda clades can be detected: derived sauropods are morphological similar to theropods in the fore limb proportions morphospace.

The most distant groups to theropods are the single specimen of Crocodylia and Artiodactyla, the A.D. to this group of mammals ranging from 0.763 to 0.959, to Ceratosauria and Carnosauria, respectively.

Comparing the morphological distances of theropods to perissodactyls and artidoactyls, one notices that, as verified in the fore limb morphospace (figure 7.3), the closest group to the carnivorous dinosaurs is perissodactyls, with A.D. ranging from 0.228, to Ceratosauria, and 0.413, to Carnosauria.

Mammalia

A consequence of artidodactyls positioning in the morphospace is the low A.D. to Crocodylia - 0.295. This morphological distance is considerable inferior to the A.D. quantified for the gap between Artiodactyla and Perissodactyla centroids - 0.557. The most distant group to Perissodactyls in the fore limb morphospace is

Dinosauromorpha - 0.705. The nearest group to Perissodactyla is Iguanodontia - 0.111, being this group of dinosaurs closer to perissodactyls than any of the mammal groups analyzed herein.

Basal Eutheria reveal proximity in the fore limb morphospace to non-Iguanodontia and Metatheria mammals, with A.D. of 0.087 and 0.121, respectively. The most distant groups to Basal Eutheria are Dinosauromorpha and Crocodylia, with A.D. of 1.255 and 1.219, respectively.

Ornithischia

Iguanodontia are closer to prosauropods than to sauropods. The least distant to these ornithischians are perissodactyl mammals, whereas the maximal distance is to dinosauromorphs, to the single specimen of crocodiles and to artiodactyls, with A.D. of 0. 0.801, 0.747 and 0.604, respectively.

Non-Iguanodontia has the lowest A.D. to Eutheria - 0.087, and is distant to dinosauromorphs, to the single specimen of crocodiles and to artiodactyls, with A.D. of 1.300, 1.270 and 1.152, respectively.

Aves

Calculating fore limb A.D. of the two Aves groups revealed that both are the closest to each other in the fore limb morphospace, 0.162, and that the morphologically most distant groups to birds are the Sauropodiformes.

Interesting is the considerable morphological distance between the bird ancestors, theropods, and these flying vertebrates, with A.D. ranging from 0.440 between non-Passerines and Coelurosauria, and 0.726 between Passerines and Carnosauria.

7.6.2 Hind limb

Theropoda

Theropods hind limb morphospace area is closely surrounded by two morphospace domains. The nearest groups to basal Theropoda and Carnosauria, in the hind limb morphospace, are basal Sauropodomorpha and Sauropodiformes, with A.D. of 0.28 and 0.29, respectively. Derived theropod groups such as Ceratosauria and Coelurosauria reveal the most morphological proximity to Dinosauromorpha (0.94) and Ceratosauria (0.57), respectively. Theropod groups are morphologically more dissimilar in the hind limb morphospace to Prototheria (basal theropods, A.D. of 0.793) and basal Titanosauria (Carnosauria, Ceratosauria and Coelurosauria, with A.D. of 0.815, 1.048 and 1.097, respectively).

Discarding intermediate A.D., one can state that the positioning of theropods is associated mainly with basal dinosaurs and other saurischians, such as prosauropods, and that theropods are located distantly to sauropods.

Mammalia

Artiodactyls reveal high morphological distances to sauropods, ranging from 0.909 to 1.254, to non-eusauropods and to basal titonasaurs, respectively. The groups closer to artiodactyls in the morphospace are the theropods Coelurosauria and Ceratosauria, with A.D. of 0.179 and 0.212, respectively.

Perissodactyla reveal patterns of morphological distances distinct to Artidoactyla, since within the limb proportions morphospace the groups located nearer to perissodactyls are Crocodylia and several sauropodomorph groups. Perissodactyls A.D. to prosauropods range from 0.218 to 0.366, in Plateosauria and basal sauropodomorphs, respectively. The morphological distances of perissodactyls to sauropods are slightly superior than to prosauropods, except to non-eusauropods

(0.204), and range from 0.361 to 0.563, in non-neosauropods and basal titanosaurs, respectively.

Basal Eutheria reveals the most morphological proximity to Prototheria and the less morphological proximity to Colerusoauria, with A.D. of 0.100 and 0.815, respectively.

Ornithischia

Non-Iguandontia show more morphological closeness to prosauropods and theropods than to sauropods or even to the other ornithischian group, the closest group being Dinosauromorpha, with an A.D. of 0.033. Similarly, the location of Iguanodontia within the morphospace is closer to both prosauropods and theropods, although the morphological distance to sauropods is slightly inferior to what was quantified in non-iguandontids.

Both ornithischian groups show hind limb proportions that are similar to prosauropods and theropods.

Aves

The Aves sample, constituted only by fossil specimens, exhibits low A.D. to derived theropods such as Ceratosauria and Coelurosauria, namely 0.071 and 0.097, respectively. A low morphological distance is also detectable between Aves and non-Iguanodontia, with an A.D. of 0.091.

The most distant positioning in the morphospace shown by fossil birds occurs towards sauropods, with A.D. ranging from 0.738 to 1.054 in non-eusauropods and basal titanosaurs, respectively.

Final remarks

The intergroup A.D. corroborate the domains identified in both limbs morphospaces - section 7.2.

The apparent incoherence of having small morphological distances between groups which present distinct types of locomotion offers new opportunities for future researches. Therefore, it will be necessary to deepen the morphological characterization of modes of locomotion and relate them to dissimilar explorations of limb proportions morphospace areas. As seen above, groups that apparently present similar types of locomotion reveal distinct morphospace occupation patterns and consequent high A.D. This fact indicates that functional and biomechanical performances are explored similarly under distinct limb proportions organizations. For example, quadrupedality implies distinct ways of exploring limb morphospaces, whereas bipedality coexists in identical areas of limb morphospaces with different modes of locomotion.

It is mandatory to deepen the description and reinterpret the various modes of locomotion, starting with the anchor point of limb proportions studies herein presented. Morphological characterizations like the one offered by techniques such as Geometric Morphometrics could constitute an appropriate methodology for the referred purposes.

Intragroups A.D.		Dino.	Prosauropoda		Sauropoda						Theropoda				Ornithsichia		Mammalia					Croco.	N. Passer.
			Plat.	Sps.	N. Eus.	N. Neos.	Diplo.	B. Macro.	B. Tita.	Lithos.	B. Thero.	Carno.	Cerato.	Coelu.	Ig.	N. Ig.	Proto.	Meta.	Euthe.	Artio.	Perisso.		
Pros.	Plat.	1.030																					
	Sps.	1.221	.196																				
Sauropoda	N.Eus.	1.053	.358	.382																			
	N.Neos.	1.008	.141	.238	.218																		
	Diplo.	.965	.146	.274	.232	.043																	
	B. Macro.	.869	.188	.357	.295	.142	.099																
	B. Tita.	.730	.308	.492	.401	.283	.241	.142															
	Lithos.	.789	.248	.432	.366	.228	.185	.086	.060														
Theropoda	B. Thero.	1.004	.247	.310	.116	.105	.116	.187	.310	.266													
	Carno.	1.007	.050	.213	.312	.094	.096	.149	.279	.219	.199												
	Cerato.	.820	.238	.409	.313	.189	.146	.052	.097	.053	.215	.200											
	Coelu.	.818	.216	.402	.366	.209	.168	.073	.092	.035	.260	.189	.064										
Orni.	Iguano.	.801	.469	.584	.271	.351	.327	.300	.298	.307	.278	.420	.271	.333									
	N. Iguano.	1.300	.380	.253	.280	.311	.353	.452	.590	.537	.296	.363	.494	.520	.548								
Mammalia	Proto.*	1.022	.417	.455	.074	.276	.281	.325	.410	.385	.170	.369	.333	.392	.224	.345							
	Meta.	1.290	.509	.432	.241	.396	.428	.513	.634	.593	.327	.477	.542	.587	.494	.195	.270						
	Euthe.	1.255	.399	.311	.212	.302	.339	.433	.565	.517	.257	.372	.469	.505	.483	.087	.269	.121					
	Artio.	.423	.999	1.158	.874	.920	.884	.811	.704	.757	.873	.959	.761	.793	.604	1.152	.819	1.081	1.086				
	Perisso.	.705	.457	.603	.349	.364	.330	.271	.219	.247	.320	.413	.228	.279	.111	.611	.317	.584	.556	.557			
Croco.*		.134	1.034	1.217	1.010	.993	.952	.861	.727	.786	.975	1.005	.809	.818	.747	1.270	.971	1.241	1.219	.295	.662		
Aves	N.Passer.	.639	.622	.762	.465	.524	.492	.436	.369	.407	.466	.577	.392	.440	.195	.742	.414	.681	.677	.410	.165	.569	
	Passer.	.671	.773	.899	.567	.665	.637	.591	.532	.567	.593	.726	.549	.601	.315	.847	.503	.753	.773	.340	.322	.573	.162

Table 7.3 Fore limb intergroups A.D. Abbreviations: Dino. – Dinosauromorpha; Plat. – Plateosauria; Sps. – Sauropodiformes; N.Eus. - non-Eusauropoda; N.Neos. - non-Neosauropoda; Diplo. – Diplodocoidea; B.Macro. - basal Macronaria; B. Tita. - basal Titanosauria; Lithos. - Lithostrotia; B. Thero. – Basal Theropoda; Carno. – Carnosauria; Cerato. – Ceratosauria; Coelu. – Coelurosauria; Ig. – Iguanodontia; N. Ig..– non-Iguanodontia; Passer. - Passerines; N.Passer. - non-Paserines; Proto. – Prototheria; Meta. – Metatheria; Euthe. - basal Eutheria; Artio. – Artiodactyla; Perisso. – Perissodactyla; Croco. – Crocodylomorpha. .*- single specimen - Prototheria: *Ornithorhynchus anatinus*; Crocodylomorpha: *Hesperosuchus agilis*).

Intragroups A.D.		Dino.	Prosauropoda			Sauropoda						Theropoda				Ornithischia		Aves	Mammalia				
			B. Sms.	Plat.	Sps.	N. Eus.	N. Neos.	Diplo.	B. Macro.	B. Tita.	Lithos.	B. Thero.	Carno.	Cerato.	Coelu.	Ig.	N. Ig.		Proto.	Meta.	Euthe.	Artio.	Perisso.
Pros.	B.Sms.	.148																					
	Plat.	.249	.154																				
	Sps.	.230	.126	.030																			
Sauropoda	N.Eus.	.641	.562	.409	.437																		
	N.Neos.	.796	.721	.567	.596	.159																	
	Diplo.	.851	.794	.639	.669	.248	.123																
	B. Macro.	.847	.773	.619	.647	.210	.052	.102															
	B. Tita.	.969	.911	.757	.786	.359	.211	.119	.167														
	Lithos.	.853	.791	.637	.666	.238	.101	.029	.074	.121													
Theropoda	B. Thero.	.138	.028	.137	.110	.546	.704	.774	.756	.892	.772												
	Carno.	.213	.098	.059	.029	.465	.624	.698	.675	.815	.695	.085											
	Cerato.	.094	.165	.305	.280	.710	.868	.930	.919	1.048	.930	.171	.256										
	Coelu.	.130	.222	.359	.335	.763	.919	.978	.970	1.097	.980	.227	.312	.057									
Orni.	Ig.	.286	.245	.114	.140	.358	.511	.566	.561	.685	.568	.220	.166	.364	.412								
	N. Ig.	.033	.167	.279	.259	.674	.829	.884	.880	1.003	.886	.161	.240	.071	.097	.319							
Aves		.113	.258	.359	.342	.738	.890	.936	.940	1.054	.941	.250	.326	.132	.113	.380	.091						
Mammalia	Proto.	.796	.821	.701	.727	.537	.539	.456	.548	.511	.483	.793	.753	.890	.918	.588	.824	.831					
	Meta.	.451	.473	.364	.388	.390	.494	.492	.533	.600	.506	.445	.411	.545	.577	.251	.481	.501	.349				
	Euthe.	.721	.735	.609	.636	.440	.456	.386	.471	.458	.411	.708	.662	.815	.847	.497	.751	.767	.100	.270			
	Artio.	.304	.347	.500	.472	.909	1.068	1.136	1.119	1.254	1.135	.364	.445	.212	.179	.573	.274	.279	1.097	.755	1.025		
	Perisso.	.464	.366	.218	.243	.204	.361	.450	.413	.563	.442	.353	.269	.523	.577	.210	.496	.570	.636	.371	.536	.713	
Croco.		.297	.234	.088	.117	.344	.500	.563	.551	.681	.563	.212	.145	.368	.419	.041	.330	.397	.615	.285	.522	.573	.178

Table 7.4 Hind limb intergroups A.D. Abbreviations: Dino. – Dinosauromorpha; B.Sms. - basal sauropodomorphs; Plat. – Plateosauria; Sps. – Sauropodiformes; N.Eus. - non-Eusauropoda; N.Neos. - non-Neosauropoda; Diplo. – Diplodocoidea; B.Macro. - basal Macronaria; B. Tita. - basal Titanosauria; Lithos. - Lithostrotia; B. Thero. – Basal Theropoda; Carno. – Carnosauria; Cerato. – Ceratosauria; Coelu. – Coelurosauria; Ig. – Iguanodontia; N. Ig. – non-Iguanodontia; Aves – Aves; Proto. – Prototheria; Meta. – Metatheria; Euthe. - basal Eutheria; Artio. – Artiodactyla; Perisso. – Perissodactyla; Croco. – Crocodylomorpha.

7.7 Disparity and size

The analyses performed in this section followed identical procedures and objectives as the ones postulated in section 6.5, namely, evaluating the relationships between the different bone parts size and the intragroup A.D. In other words, the goal is to analyze the existence of a relationship between absolute size and the proportions disparity among the analyzed groups. The results are depicted in table 7.5 and figure 7.7.

Groups	n fore hind	Size (log length) H r	H p	R r	R p	MC r	MC p	F r	F p	T r	T p	MT r	MT p
Dinosauromorpha	n=1 n=7	a	a	a	a	a	a	+	n.s.	+	n.s.	+	n.s.
Basal Theropoda	n=2 n=6	a	a	a	a	a	a	-.743	.045*	-.755	.043*	-	n.s.
Carnosauria	n=1 n=16	a	a	a	a	a	a	-	n.s.	-	n.s.	-	n.s.
Ceratosauria	n=2 n=19	a	a	a	a	a	a	.534	.019	.522	.022	.488	.034
Coelurosauria	n=6 n=68	+	n.s.	+	n.s.	+	n.s.	+	n.s.	+	n.s.	+	n.s.
Aves	n=0 n=18	c	c	c	c	c	c	+	n.s.	.452	.030*	.450	.031*
Iguanodontia	n=11 n=15	-.689	.019	-.674	.023	-.697	.017	-.638	.010	-.674	.006	-.614	.015
Non-Iguanodontia	n=1 n=14	a	a	a	a	a	a	+	n.s.	+	n.s.	+	n.s.
Metatheria	n=32 n=16	-	n.s.	-	n.s.	-	n.s.	.749	.001	.841	<.001	.895	<.001
Artiodactyla	n=65 n=66	-	n.s.	-.229	.034*	-.265	.033	.264	.032	+	n.s.	+	n.s.
Perissodactyla	n=24 n=33	+	n.s.	+	n.s.	-	n.s.	.452	.008	.562	.001	.297	.047*

Table 7.5 Correlations of intragroups A.D. and log transformed length of limb parts - see text. *- significant one-tailed; a - one/two specimen(s); b - no specimens with three preserved parts; c - not analyzed; n.s. - non significant, p>0.05; r - Pearson coefficient; p - p value, significance.

7.7.1 Fore limb

Due to the small sample size of theropod fore limb parts, only the bivariate correlation analyses on coelurosaurian individuals was performed. Among this group of theropods, correlation coefficients were not significant for all fore limb parts, but revealed a positive correlation signal of A.D. and size. This suggests that larger coelurosaurs have higher A.D., that is to say, larger coelurosaurs individuals are more spread out in the fore limb proportions morphospace than smaller coelurosaurs

individuals, which have lower disparity indexes. In other words, large coelurosaurs explore the fore limb morphospace more widely than smaller coelurosaurs, which are more conservative in terms of fore limb proportions.

Metatheria specimens revealed non-significant and negative correlations of A.D. and size for all bone parts, and bivariate correlations performed on the metatherian larger forms sub-sample (fore limb larger than 150 mm, n = 12) revealed negative correlations of A.D. in all bone parts sizes, showing significant values only in the humerus $r = -0.590$, $p = 0.044$. This implies that, within the largest metatherian sub-sample, the fore limb proportions morphospace is occupied in a narrower way than the one of smaller metatherian forms. The bivariate correlation analyses carried out on the metatherian smaller forms sub-sample (fore limb smaller than 150 mm, n = 20) revealed somewhat distinct results to the complete and larger metatherian samples, since correlation signals of radius and metacarpal are positive, although not significant. These results entail that the relationship between A.D. and size is not identical in larger and smaller metatherians and this difference in morphospace positioning could be attributable to the radius and metacarpal proportions.

Artiodactyls show negative correlations of A.D. and size for the entire fore limb bone parts, being non-significant only in the humerus. Artiodactyl smaller forms sub-sample (fore limb smaller than 500 mm, n = 25) revealed negative correlations of A.D. and bone parts sizes, being significant only for the metacarpal size - $r = -0.512$, $p = 0.009$. These results indicate that the smallest artiodactyl individuals are more distant to its group morphospace centroid, that is to say, smaller forms occupy the proportions morphospace in a wider way than artiodactyl larger forms and, consequently, are more disparate in terms of fore limb proportions than larger forms. Artiodactyl larger forms sub-sample (fore limb larger than 500 mm, n = 40) revealed non-significant and negative correlations of A.D. and bone parts sizes, thus revealing an inverse relationship of A.D. and size.

Perissodactyls reveal a relationship of A.D. and size different from artiodactyls, since in the former group positive correlations in humerus and radius, as negative correlations in the metacarpal and A.D., were identified. Perissodactyl larger forms sub-sample (fore limb larger than 900 mm, n = 6) showed non-significant correlations for A.D. and size, although with distinct correlation signals among the bone parts - positive for the metacarpal size and negative for humerus and radius sizes. Perissodactyla smaller forms (fore limb smaller than 800 mm, n = 18) also presented non-significant correlations for A.D. in all bone parts, but the correlations are positive for A.D. in all bone sizes. Thus, the larger and smaller perissodactyl sub-samples reveal distinct ways of fore limb morphospace occupation: bigger perissodactyls forms are more conservative in the fore limb proportions morphospace in what concerns humerus and radius sizes, but are more disparate regarding metacarpal size, while smaller perissodactyls show a distinct relationship of A.D. and size.

Regarding ornithischians, the correlation analyses on Iguanodontia revealed significant and negative correlations of A.D. on all bone parts sizes. This result implies that, within the complete sample, larger iguanodontids are less disperse in the fore limb proportions morphospace than smaller iguanodontid individuals, since the latter group reveals higher A.D. Identical correlation analyses were performed on the smaller iguandontid individuals (fore limb length smaller than 1400 mm, n = 5), revealing significant and strong negative correlations of A.D. and size for all bone parts - humerus r = -0.974, p = 0.005; radius r = -0.941, p = 0.017; metacarpal r = -0.949, p = .014. These results put in evidence that, within the smaller iguanodontids sub-sample, there is an evident and strong relationship between the disparity index A.D. and size on all the fore limb parts. This means that the smallest iguanodontids are more disparate in fore limb proportions morphospace than the larger ones. The complementary analysis of iguanodontian sub-sample, that is to say, the sub-sample of larger individuals (fore limb length larger than 1400 mm, n = 6) reveals non-significant

and negative correlations of A.D. and size for the humerus and metacarpal; the correlation coefficient signal for the radius is positive, although non-significant, a divergent trend to the one observed in iguanodontian complete and smaller individuals samples. It seems, therefore, that the radius proportion is a discordant bone part and is altering the relationship of A.D. and size in larger iguanodontids sub-sample.

7.7.2 Hind limb

In theropods it is possible to identify a significant correlation in some groups, namely in basal Theropoda and Ceratosauria, although with opposite influences of size on A.D.; basal theropods exhibit a strong negative correlation between the A.D. and femur and tibia lengths, while Ceratosauria exhibit strong positive correlations between A.D. and femur and tibia lengths. Performing bivariate correlation analyzes only on bigger Carnosauria individuals (hind limb length bigger than 2000 mm sample, n = 8), the correlations coeffcients remain non-significant, although in the tibia and metatarsal parts they turn positive. The bivariate correlation analyses performed on Carnosauria smaller individuals (hind limb length smaller than 2000 mm, n = 8) reveal different results than the larger individuals sub-sample; significant and strong negative correlations of A.D. and bone parts could be identified - femur r = -0.796, p = 0.018; tibia r = -0.720, p = 0.044; metatarsal r = -0.712, p = 0.047. This implies that, within the smaller carnosaur sub-sample, when bone size increases a lower A.D. emerges, that is to say, smaller Carnosauria individuals reveal a wider morphospace occupation pattern.

Analyses of Ceratosauria larger species (hind limb length larger than 500 mm, n = 10) revealed positive and stronger correlation coefficients of A.D. and size than the complete sample - femur r = .880, p = .001; tibia r = .831, p = .003; metatarsal r = .729, p = .017. This implies that, among the largest ceratosaurs sub-sample, the A.D. is higher than in smaller forms, that is to say, ceratosaur larger forms occupy the hind limb proportions morphospace wider than smaller forms. Correlation analyses of the

smallest ceratosaur forms (hind limb length smaller than 500 mm, n = 9) showed correlations coefficients equivalent to ceratosaur larger forms, except in the autopodial element, where A.D. and metatarsal size are negatively correlated, although not significantly: femur r = .814, p = .008; tibia r = .738, p = .023.

Regarding the reevaluation of Coelurosauria larger species (hind limb length larger than 1000 mm, n = 24), it can be observed that correlation coefficients are all not-significant and that, in the tibia and metatarsal, opposite correlation signals (i.e., negative) to those of the complete sample were noticeable. Corresponding results may be detected in the smaller coelurosaurs sub-sample (hind limb length smaller than 1000 mm, n= 44), except for the metatarsal, where there is a negative correlation of A.D. and size.

The Aves hind limb sample revealed that tibia and metatarsal lengths are significantly and positively correlated with A.D, the femur revealing a positive although non-significant correlation with A.D. This way, larger bird species occupy the hind limb proportions morphospace more extensively than smaller birds.

Ornithopods reveal distinct correlation patterns among the analyzed groups; Iguanodontia individuals display significant and strong negative correlations in all the three hind limb bones, while non-Iguanodontia individuals do not show significant correlations in any of the hind limb bones. The evaluation of A.D. and size among larger iguanodontid species (hind limb length larger than 1000 mm, n = 10) showed that all bone correlations become non-significant, although revealing similar and lower correlation signals to the complete sample, that is to say, a negative correlation of A.D. and size. The equivalent bivariate correlation analysis performed on larger non-iguanodonts (hind limb length larger than 300 mm, n = 8) showed identical results as the complete non-iguanodontid sample, that is to say, positive and non-significant correlation of A.D. and size in all hind limb bones. Smaller non-iguanodontids sub-

sample (hind limb length smaller than 300 mm, n = 6) revealed equivalent results as the larger and complete non-iguanodontids samples.

Metatheria show significant and strong positive correlations with A.D. in all three bone parts, being the mammal group the one which shows a stronger relationship between the disparity index and the size of bone parts.

Artiodactyls demonstrate a positive and significant correlation coefficient only between A.D. and femur length, and non-significant, although positive, correlation coefficients in tibia and metatarsal lengths. The computation of the bivariate correlation on the larger artiodactyls sub-sample (hind limb length greater than 900 mm, n = 10) revealed that correlation coefficients increase substantially - femur r = .791, p = .006; tibia r = .791, p = .007; metatarsal r = .861, p = .001. This fact means that the biggest individuals present higher A.D. and, therefore, explore the hind limb proportions morphospace more extensively than smaller artiodactyl forms. The correlation analyses performed on the smaller artiodactyl sub-sample (hind limb length smaller than 900 mm, n = 56) reveal positive and non-significant correlations of A.D. and femur and tibia sizes and negative and a non-significant correlation with metatarsal size. This result seems to indicate that the exploration of wider morphospace areas is performed distinctively by larger and smaller artiodactyl species, namely in what concerns the metatarsal.

Perissodactyl mammals reveal positive correlations with A.D. in all the three hind limb bones. Analyzing only perissodactyl bigger forms (hind limb length larger than 900 mm, n = 15), it could be detected that correlation coefficients are superior to the complete sample - femur r = .616, p = .014; tibia r = .678, p = .005. Concerning the metatarsal length correlation with A.D. within the larger perissodactyl forms, it was verified that, oppositely to the results in the complete sample, the correlation, although positive, is not significant. Therefore, the larger perissodactyl species sub-sample shows bigger A.D. than smaller forms, implying that bigger perissodactyl forms explore

the hind limb proportions morphospace more broadly than smaller forms, which remain in a confined area of the morphospace. The perissodactyl sub-sample of smaller forms (hind limb length smaller than 900 mm, n = 18) revealed that correlation coefficients of A.D. and all bone parts sizes are negative, although non-significant.

7.7.3 General trends

Concerning theropod groups, it is noticeable that, in the hind limb proportions, the basal groups, like basal Theropoda and Carnosauria, reveal a trend of morphospace occupation opposite to the one verified in derived forms, such as Ceratosauria or Coelurosauria. If basal groups show that smaller forms are more disparate in hind limb proportions than larger forms, more derived groups reveal the contrary, that is to say, larger forms are more disparate. Although displaying a similar pattern of locomotion, basal and derived theropod groups show distinct patterns of hind limb morphospace occupation. If this consideration is complemented with the fore limb morphospace data, and regarding only coelurosaurs, it is possible to identify an identical relationship of A.D. and size, allowing to state that, in derived theropods, size matters, that is to say, the bigger the animal the more disparate the proportions. An identical general trend was identified for Aves hind limb, that is, the bigger the bird the more disparate it is.

The relationships between A.D. and bone parts sizes in each limb are identical and positive for Perissodactyla, that is to say, bigger forms in both limbs show higher A.D. Larger perissodactyls show a wider occupation in both fore and hind limb morphospaces than smaller perissodactyls and, therefore, one could state that size in perissodactyls is correlated to limb proportions disparity.

The relationship of size and disparity in artiodactyls revealed that bigger animals are more disparate than smaller ones in the hind limb, but there is an opposite relationship of size and disparity in the fore limb. The analysis of smaller forms sub-sample showed an opposite metatarsal proportion relationship with size than the

observed in bigger artiodactyls. This reveals that the exploration of hind limb morphospace changed in the metatarsal of smaller artiodactyls.

Metatheria and Artiodactyla show opposite relationships of A.D. and size in fore and hind limbs, that is to say, in the fore limb one verifies that smaller animals reveal higher A.D., while in the hind limb larger forms reveal higher A.D. Therefore, in these groups of mammals, disparity and size have distinct relationships in the two limbs.

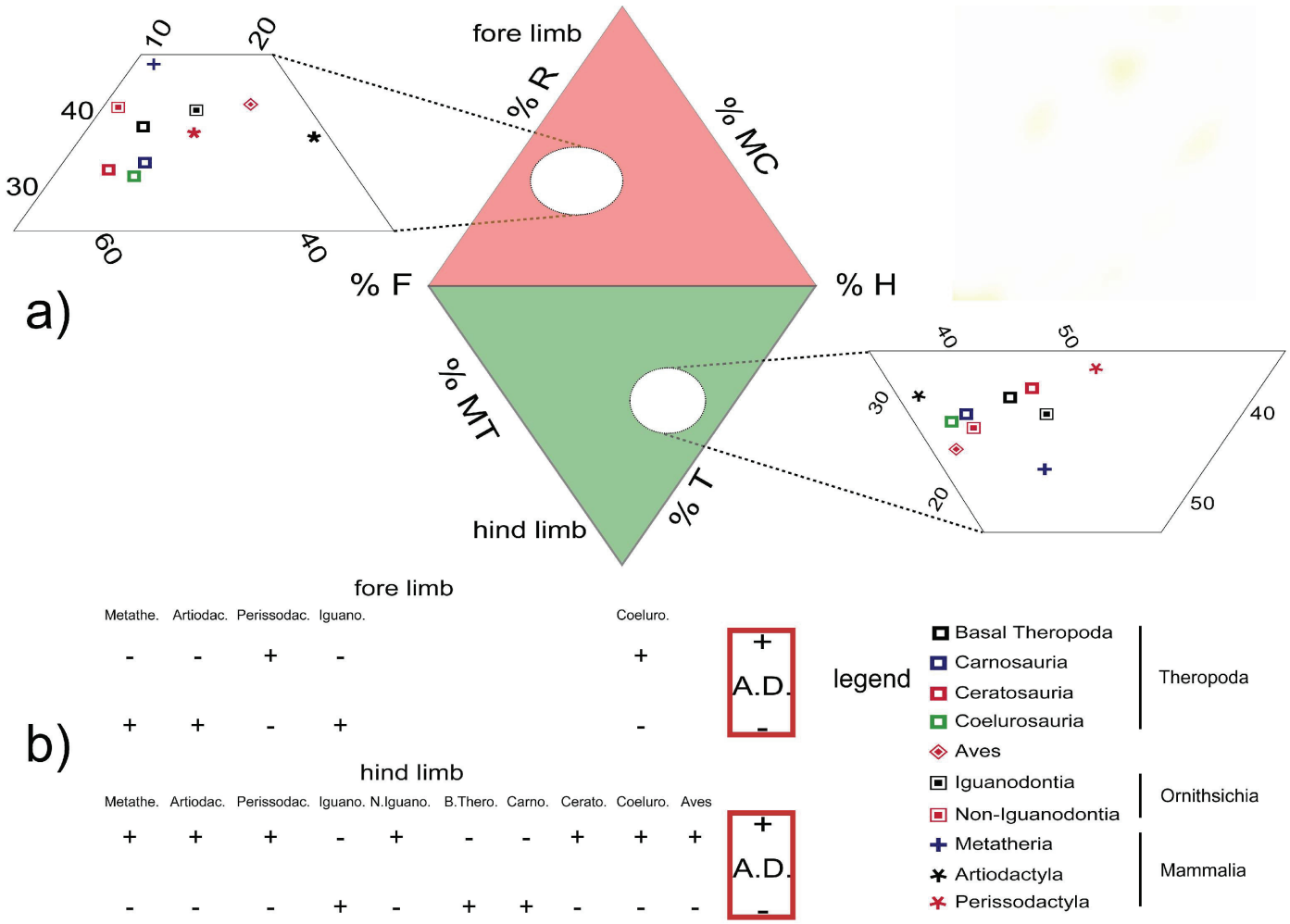

Figure 7.7 a) Mammals, Theropoda and Aves fore and hind limbs morphospaces with groups centroids. b) Graphical illustration of the bivariate correlations between A.D. and size quantified in table 7.5.

7.8 Biplots

The biplot analyses performed in this section followed identical methodological steps as described in sections 2.2.7 and 6.6. The biplots concerning the relationship among limb parts of the two groups are depicted in figure 7.8.

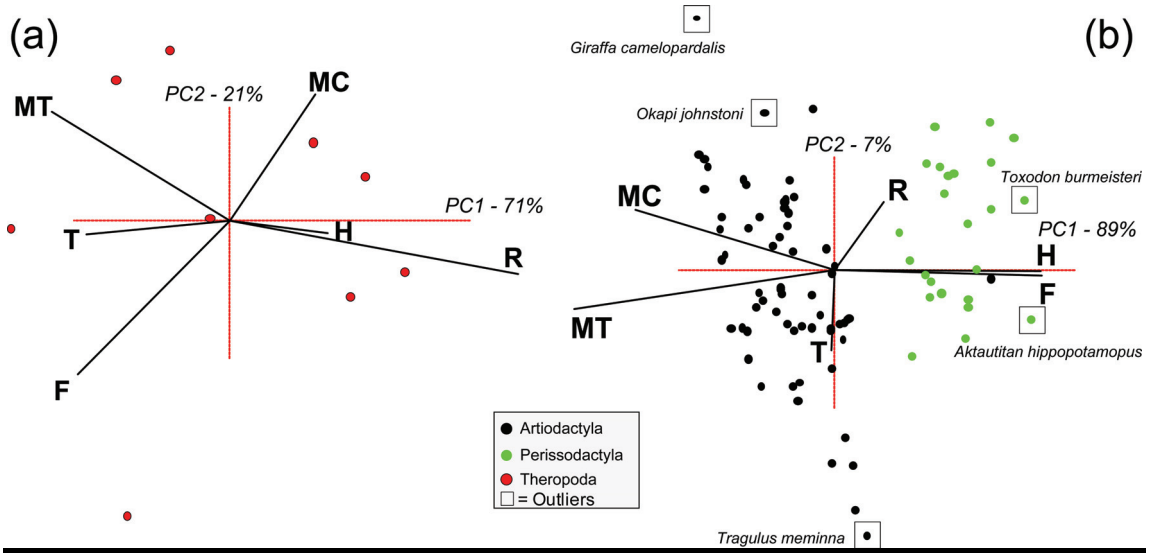

Figure 7.8 a) Biplot of the *clr*-transformed space of the first two principal components (PC1 vs PC2) of Theropoda dinosaurs. First Principal Component (71%), Second Principal Component (21%). Third Principal Component (7%), Fourth Principal Component (0.6%) and Fifth Principal Component (0.4%). There is any outlier. b) Biplot of the *clr*-transformed space of the first two principal components (PC1 vs PC2) of Artiodactyla and Perissodactyla mammals . First Principal Component (89%), Second Principal Component (7%), Third Principal Component (2%), Fourth Principal Component (1%) and Fifth Principal Component (1%).

7.8.1 Theropoda

Theropod dinosaurs reveal a total explained variance that sums 92%, for the two first principal axes. PC1 is mostly controlled by the log-ratios of radius, tibia and humerus and PC2 is influenced by the autopodial bones and the femur. One should mention that the links of radius and metatarsal, as well as the links of the humerus and metatarsal, are approximately orthogonal to the link of femur and metacarpal. This implies that the ratio of radius-metatarsal and humerus-metatarsal are independent from the ratio of femur-metacarpal, or that the correlation of those log-ratios is approximately zero. These relationships among the theropods bone parts could be

completed with the analysis of the variation array depicted in table 7.6. Theropods reveal most of their variability in the radius, followed by the femur and metatarsal.

Another particularity of theropods biplots is the approximate collinearity of the rays of the variables radius, humerus, metatarsal and tibia. As seen in chapters 2 and 6, the collinearity of those rays indicates that their variability is mainly one-dimensional, which could be confirmed by a principal component analysis of the parts. This analysis could be the scope of future studies.

7.8.2 Mammalia

The relationship among bones in the two mammals groups allows identifying that femur, humerus and metatarsal are the main factors influencing PC1, which explains an enormous percentage of the total variability – 89%. This axis of variation is also influenced by another important bone proportion - metacarpal, which, although less directly than the previously mentioned bones, shows a large ray, which reveals a significant source for the sample total variability. PC2 has, comparatively to PC1, an extremely low value in the explanation of the total variation, being influenced firstly by the tibia and secondarily by the metacarpal.

Since within the mammals biplots the vertices of femur and tibia are nearly coincident, this means that the variance [ln(tibia/femur)] is zero, or nearly so, in turn implying that the ratio Xtibia/Xfemur is almost constant - approximately 1.026.

Observing the two groups specimens dispersion, the separation of the two clusters along PC1 is clearly detectable, which is, as stated above, determined mainly by the femur, humerus and metatarsal proportions. Therefore, if one represents Artiodactyla and Perissodactyla specimens in a ternary morphospace of femur, humerus and metatarsal proportions, one will have a clear separation of the two groups.

Table 7.6 represents the variation array of the two mammals groups. It is recognizable that metatarsal is the main source of relative variability within individuals,

followed by the metacarpal, femur, humerus, radius and tibia, with percentages of 24.3, 18.5, 18.4, 18.2, 10.4 and 10.2, respectively. If one sums the mammals fore limb parts relative one will obtain a percentage of variance of 47.1 being, therefore, slightly more variable in the fore limb than in the hind limb.

	Theropoda (n=9)								Artiodactyla+Perissodactyla (n=87)							
	H	R	MC	F	T	MT	*clr* var	% var	**H**	**R**	**MC**	**F**	**T**	**MT**	***clr* var**	**% var**
H		.030	.030	.069	.048	.069	.021	**11.0**		.038	.195	.003	.061	.252	.046	**18.2**
R	.460		.064	.159	.144	.186	.049	**25.9**	-.038		.079	.042	.030	.126	.026	**10.4**
MC	1.219	.759		.101	.061	.071	.027	**14.6**	.285	.323		.196	.069	.021	.047	**18.5**
F	-.793	-1.253	-2.012		.017	.059	.034	**18.0**	-.251	-.213	-.536		.062	.253	.046	**18.4**
T	-.793	-1.254	-2.013	-.001		.016	.024	**12.7**	-.225	-.187	-.510	.026		.084	.025	**10.2**
MT	-.224	-.684	-1.443	.569	.569		.033	**17.8**	.240	.278	-.045	.492	.465		.061	**24.3**
Total variance = .1874									**Total variance = .2518**							

Table 7.6 Variation arrays for Dyke et al. 2006 Theropoda and Artiodactyla+Perissodactyla data set. Abbreviations: H - humerus; R – radius; MC – metacarpal III; F – femur; T – tibia; MT – metatarsal III.

7.9 Statistical tests

Analogously to what was performed in section 6.7, the disparity index A.D. group differences was tested by means of ANOVA. The test was performed with intragroup A.D. and informs on how the elements of a group are distributed within the morphospace, that is to say, the pattern of specimens distribution in the morphospace.

7.9.1 Theropoda fore limb

Due to the reduced sample size of theropod groups, it was not possible to perform the ANOVA.

7.9.2 Theropoda hind limb

The ANOVA test revealed that there are significant differences in the intragroups mean A.D. among the four compared groups, Basal Theropoda, Carnosauria, Ceratosauria and Coelurosauria: $F= 5.54$; $p= 0.001$. In other words, the theropod groups, besides further occupying different areas of the hind limb morphospace, fill the respective domains in different ways.

The four mammal groups different occupation patterns of the morphospace was confirmed by the Kruskal-Wallis nonparametric test, which compares medians of A.D.: H = 45.63; p= 0.000.

7.9.3 Mammalia fore limb

The ANOVA test revealed that there are significant differences in the intragroups mean A.D. among the three compared groups, Metatheria, Artiodactyla and Perissodactyla: F = 103.73; p = 0.000. This implies that the distribution patterns of the mammal groups analyzed reveal different behaviors. In other words, perissodactyls, artiodactyls and metatherians, besides occupying different areas of the fore limb morphospace, fill the respective domains differently. The three mammal groups different occupation patterns of the morphospace was confirmed by the Kruskal-Wallis nonparametric test, which compared medians of A.D.: H = 64.58; p= 0.000.

Prototheria and basal Eutheria were not tested, due to reduced sample size.

7.9.4 Mammalia hind limb

The ANOVA test revealed that there are significant differences in the intragroups mean A.D. among the three groups compared: Metatheria, Artiodactyla and Perissodactyla - F= 30.99; p= 0.000. This implies that the distribution patterns of the mammal groups analyzed reveal different behaviors. In other words, perissodactyls, artiodactyls and metatherians, besides occupying different areas of the hind limb morphospace, fill the respective domains in different ways. The three mammal groups different occupation patterns of the morphospace was confirmed by the Kruskal-Wallis nonparametric test, which compared medians of A.D.: H = 45.63; p= 0.000.

Prototheria and basal Eutheria were not tested due to reduced sample size.

7.10 Balances

A theoretical background of balances analysis was introduced in chapters 2 and 3, in which examples of applications were performed and described in detail. Section 6.8 also presents a sauropodomorphs balances analysis.

In the present section, a balances analysis of different groups with specimens that have six preserved bones and including prosauropods (Plateosauria and Sauropodiformes), basal sauropods (non-Neosauropoda and non-Eusauropoda), Diplodocoidea, derived sauropods (basal Titanosauria, basal Macronaria and Lithostrotia), mammal groups such as Artiodactyla and Perissodactyla and theropod dinosaurs was performed.

Group selection was determined primarily by two sorts of reasons: allowing a broad comparison of limb proportions variability and having a reasonable number of specimens, thus permitting a minimum sample size for each group. The number of specimens for each group is indicated in table 7.1.

The following partitions of the sauropodomorphs sample have been used in the balances analysis mainly to allow a comparison between both limbs and also the comparison among the homologous appendicular modules, as well as to allow performing intra-limb comparisons. The balances are explained in table 7.7.

Balance	H	R	MC	F	T	MT	Anatomical/Analytical meaning
B1	**1**	**1**	**1**	**-1**	**-1**	**-1**	fore limb vs. hind limb
B2	**1**	**1**	**-1**	**0**	**0**	**0**	humerus and radius vs. metacarpal
B3	**1**	**-1**	**0**	**0**	**0**	**0**	humerus vs. radius
B4	**0**	**0**	**0**	**1**	**1**	**-1**	femur and tibia vs. metatarsal
B5	**0**	**0**	**0**	**1**	**-1**	**0**	femur vs. tibia

Table 7.7 Sequential binary partition (SBP) used in the balance Table 7.8 – Sequential binary partition (SBP) used in the balance dendrogram illustrated in figure 7.9. Parts: F – femur; H – humerus; MC – metacarpal III; MT – metatarsal III; R – radius; T – tibia.

The computed balances for each sample are as follows:

$$B1 = \sqrt{\frac{3\cdot 3}{3+3}} \ln \frac{(F\cdot T\cdot MT)^{1/3}}{(H\cdot R\cdot MC)^{1/3}},\ B2 = \sqrt{\frac{2\cdot 1}{2+1}} \ln \frac{(H\cdot R)^{1/2}}{(MC)^{1/1}},\ B3 = \sqrt{\frac{1.1}{1+1}} \ln \frac{(H)^{1/1}}{(R)^{1/1}},$$

$$B4 = \sqrt{\frac{2.1}{2+1}} \ln \frac{(F\cdot T)^{1/2}}{(MT)^{1/1}}, B5 = \sqrt{\frac{1.1}{1+1}} \ln \frac{(F)^{1/1}}{(T)^{1/1}}.$$

The following table depicts the decomposition of the variances of these balances, both for balances, groups and within groups:

Balances	Plat. + Sps. n= 83		N.Eus. + N. Neo. n= 5		Diplo. n= 3		B. Tita. + B. Macro. + Lithos. n= 8		Artio. n= 63		Perisso. n= 24		Thero. n= 9		var total (by balance)	var % (by balance)
	var	**%**	**var**	**%**	**var**	**%**	**var**	**%**	**var**	**%**	**var**	**%**	**var**	**%**		
B1 (fore vs hind limb)	.043	**21.9**	.018	**9.2**	.001	**0.5**	.013	**6.6**	.011	**5.6**	.007	**3.6**	.103	**52.6**	.195	**36.1**
B2 (H and R/U vs MC)	.015	**12.6**	.004	**3.4**	.011	**9.2**	.018	**15.1**	.038	**31.9**	.010	**8.4**	.023	**19.3**	.119	**22.1**
B3 (H vs R/U)	.006	**10.9**	.007	**12.7**	.004	**7.3**	.003	**5.5**	.013	**23.6**	.008	**14.5**	.014	**25.5**	.054	**10.0**
B4 (F and T vs MT)	.006	**4.9**	.019	**15.6**	.008	**6.6**	.020	**16.4**	.031	**25.4**	.018	**14.8**	.020	**16.4**	.122	**22.6**
B5 (F vs T)	.004	**8.2**	.003	**6.1**	.008	**16.3**	.006	**12.2**	.009	**18.4**	.012	**24.5**	.007	**14.3**	.050	**9.2**
var TOTAL (by groups)	.075		.050		.032		.060		.102		.055		.167		**Total variance**	
var % (by groups)	**13.9**		**9.2**		**5.9**		**11.1**		**18.8**		**10.3**		**30.8**		0.540	

Table 7.8 Sauropodomorpha, Theropoda and Mammalia balances variance decomposition. Variances are indicated as absolute values and percentages for: balance, group and within groups. Balances indicated in Table 4.8. Abbreviations Plat. – Plateosauria; Sps. – Sauropodiformes; N.Eus. - Non-Eusauropoda; N.Neos. - Non-Neosauropoda; Diplo. – Diplodocoidea; B.Macro. - Basal Macronaria; B. Tita. - Basal Titanosauria; Lithos. - Lithostrotia; Thero. – Theropoda; Artio. – Artiodactyla; Perisso. – Perissodactyla.

7.10.1 Balances – complete sample

Observing table 7.8 and the corresponding balance dendrogram – figure 7.9, in which the variance decomposition of balances is represented, one notices that the balance that mostly contributes to the total variance is B1 (36.1%), followed by the homologous balances pairs – B2-B4 and B3-B5 – with comparable total variances among pairs.

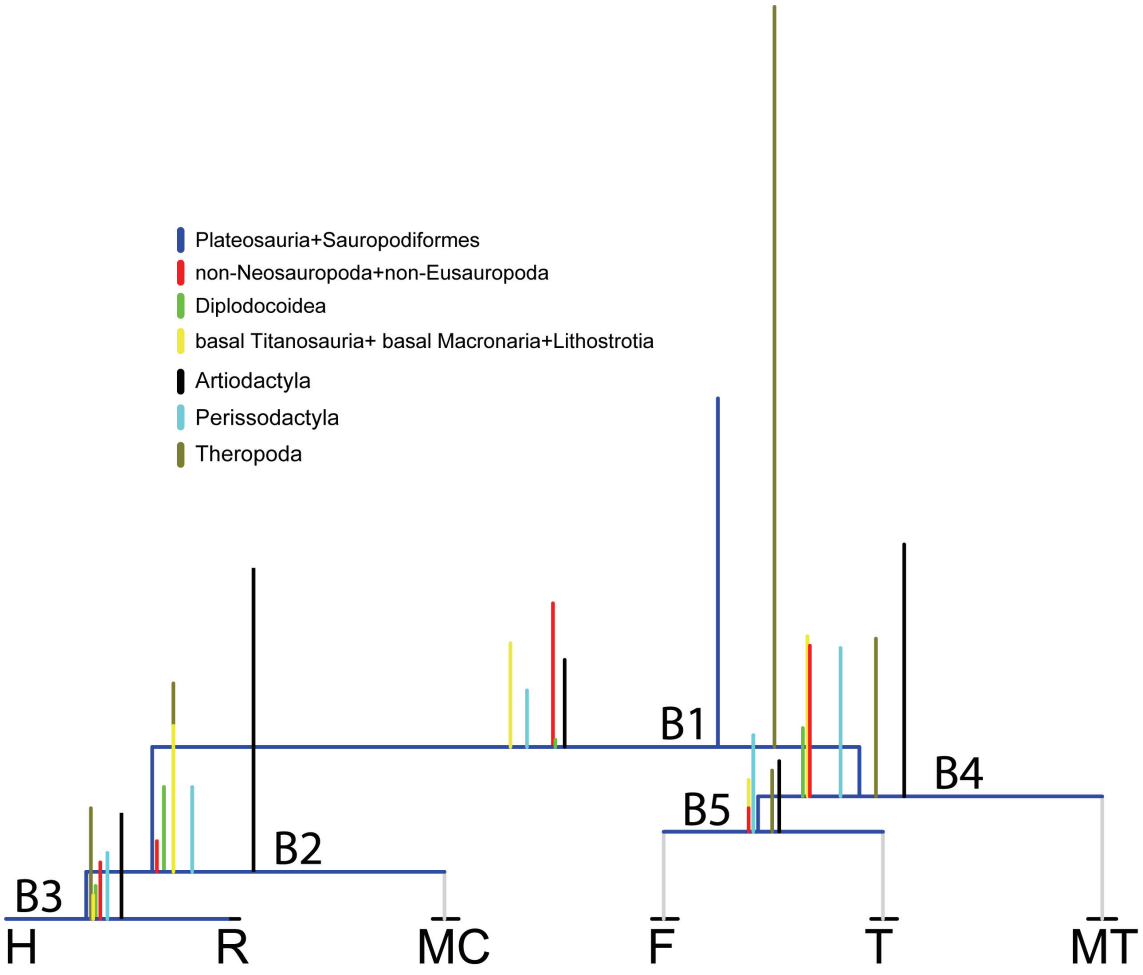

Figure 7.9 Balances dendrogram of groups of vertebrates. Sequential binary partition indicated in Table 7.7. Balances variance decomposition are represented in table 7.8. Parts: F – femur; H – humerus; MC – metacarpal III; MT – metatarsal III; R – radius; T – tibia.

7.10.2 Balances - within groups

If one emphasizes the relative importance of balances within groups, one realizes that balance B1 – fore vs. hind limb - is still the most important balance in theropods (52.6%) and prosauropods (21.9%), groups which are considered as bipedals, or at least facultative bipedals in the case of 'prosauropods'. Balance B1 results seem to indicate that in prosauropods and theropods both limbs are poorly integrated, that is to say, since there is high variation among limbs, the morphological integration between fore and hind limbs is low. Whether or not this statement is sufficient to classify the bipedal condition should be subjected to future analyses.

In the other groups, which do not show B1 as the main source of variability, B1 ranges from the minimum percentage of variance in Diplodocoidea[1] (2.6%) to a higher percentage in primitive sauropods (non-Neosauropoda+Non-Eusauropoda, 21.3%). In derived sauropods, such as basal Titanosauria, basal Macronaria and Lithostrothia, the relative influence of the variability of balance B1 reveals a considerable degree of morphological integration between limbs.

In the Saurischia sample (sauropodomorphs and theropdods), one identifies an increase of variability between fore and hind limb along the clade to derived sauropods, that is to say, the variance of B1 decreases from Theropods to prosauropods and within the Sauropoda clade. One could state, therefore, that there is an increase of morphological integration along the Saurischia clade.

In mammals, the variance attributed to B1 is reduced in both groups. Perissodactyla (3.6%) and Artiodactyla (5.6%) exhibit low variance among limbs, thus revealing a high morphological integration among limbs, which is somewhat comparable to derived sauropods (6.6%).

Concerning B3, which results from the comparison of the fore limb stylopodium and zeugopodium bones (humerus vs. radius), the group in which this balance contributes more to the total variance is Theropoda (25.5%), followed by Artiodactyla (23.6%) and Perissodactyla (14.5%). Sauropodomorphs reveal low variability between humerus and radius, whereas prosauropods are the group with more variability (10.9%), a reduction of variability being observable within the Sauropoda clade. One could state that theropods and mammals reveal a low degree of morphological integration of humerus and radius proportions when compared to sauropodomorph groups, which show higher morphological integration between the cited bones. As stated in previous sections, balance B3 is an indicator of the brachial

[1] Diplocoidea sample is only constituted by three specimens and by two species being this low sampling, both in number of specimens and species, probably the main reason of this extremely low variance in B1 – 2.3%.

index, the present balances analysis revealing that the variability of the brachial index is higher in theropods and mammals than in sauropodomorphs and, among this latter group, higher in ‘prosauropods’ than in sauropods.

Balance B5 results reveal that mammal groups show most of the variability between femur and tibia proportions. Perissodactyla is the group showing most variability (24.5%), followed by Artiodactyla (18.4%). Balance B5 results also show that, within sauropods, higher variability is present in Diplodocoidea (16.3%) and that there is an increase of variability in the Sauropoda clade, ranging from 8.2 to 12.2%, in primitive and derived sauropod groups, respectively.

7.11 Final Remarks

The present chapter evaluated limb proportions of distinct groups. Both morphospace occupation patterns and disparity measures were quantified.

One of the objectives of this study is to improve the characterization of bipedal and quadrupedal limb proportions morphospaces and to quantify the disparity differences among distinct tetrapod groups.

The distinct methods applied in chapters 6 and 7 allowed to recognize some trends:

Bipedality

- distinguish better saurischian bipedal locomotion in the hind limb morphospace than in the fore limb; saurischian bipedal locomotion is better distinguishable in the hind limb morphospace than in the fore limb;

- the two modes of locomotion among prosauropods and sauropods could be more deeply linked to the hind limb proportions than previously thought;

- the level of morphological integration between fore and hind limbs is very low in Theropoda, Prosauropoda and Metatheria;

- the hind limb morphospace allows better identification of saurischian bipedal locomotion than the fore limb morphospace, despite the existence of a distinctive saurischian morphospace area, which is more evident in the fore limb proportions than in the hind limb proportions.

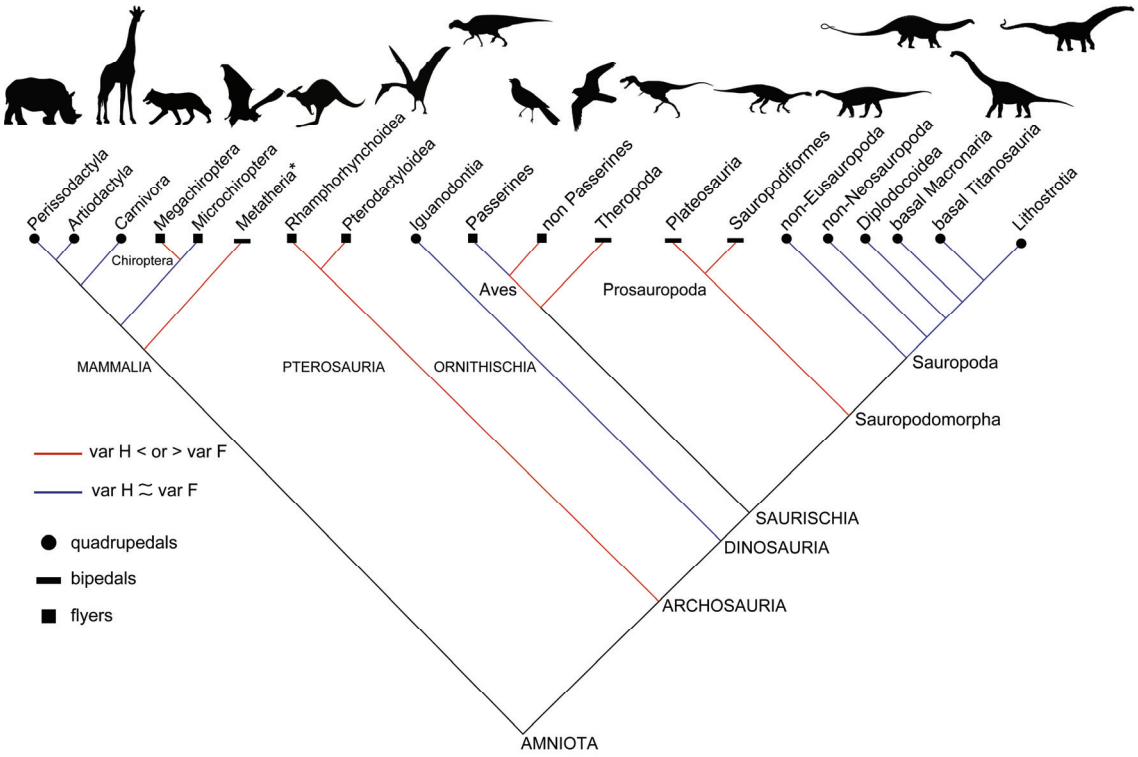

Figure 7.10 Analyzed groups simplified cladogram illustrating the relationship of locomotion type and *clr* variances of humerus and femur. Variances indicated in table 7.9. * - Metatheria sample constituted only by Diprotodonta specimens - kangaroos.

Quadrupedality

- distinct areas of quadrupedal locomotion in the proportions morphospaces can be identified, that is to say, quadrupedality implies distinct ways of exploring limb morphospaces;

- sauropods reveal two patterns of fore limb morphospace occupation - one for basal sauropods and another for derived sauropods;

- Metatheria, Artiodactyla and Iguanodontia present a relationship of size and fore limb morphospace occupation similar to that of derived sauropods;

- the Artiodactyla and Perissodactyla biplots allowed to identify that

stylopodium (humerus and femur) and zeugopodium (metacarpal and metatarsal) are the bone parts that permit to distinguish the two groups specimens;

Size

- an increase in size implied, in sauropods, a wider occupation of hind limb morphospace;

- Metatheria, Artiodactyla, Perissoadctyla, Theropoda and non-Iguanodontia reveal a relationship of size and hind limb morphospace occupation identical to derived sauropods, except Lithostrotia;

- theropods revealed two trends in the relationship of size and hind limb morphospace occupation: one for primitive theropods and another for derived theropods.

Morphological Integration

The *clr* variance analyses, compiled in table 7.9 and depicted in figure 7.10, permit to identify some numerical characterization of three types of locomotion, concerning limb elements proportions:

- in quadrupedals, such as sauropods, iguandontids and mammals (perissodactyls, artiodactyls and carnivores), the *clr* humerus and femur proportions variances are identical or sub-identical. This fact seems to indicate a high level of morphological integration between the humerus and the femur in quadrupedals.

- in bipedals, such as theropods, prosauropods and metatherians (kangaroos), the *clr* humerus proportions variance is considerable inferior to the *clr* femur proportion variance. This fact seems to indicate a low level of morphological integration between the humerus and the femur in bipedals.

Locomotion	Taxa	var **H**		var **F**		var **B1**
		Combined sample	Individual sample	Combined sample	Individual sample	
Quadrupedals	Artio. + Perisso.	.046 (18.2%)	Artio. .018 (17.1%) Perisso. .010 (17.4%)	.046 (18.4%)	Artio. .018 (17.1%) Perisso. .010 (17.5%)	Artio. .011 (5.6%) Perisso. .007 (3.6%)
	Sauropoda	.009 (12.6%)	N.Eus. N. Neo. .011 (17.2%) Diplo.# : .004 (8.6%) Tita. Macro. Lithos. .008 (12.2%)	.010 (13.5%)	N.Eus.+ N. Neo. .010 (15.4%) Diplo.# .011 (23.4%) Tita. Macro. Lithos. .008 (11.9%)	N.Eus.+ N. Neo. .018 (23.8%) Diplo.# .001* (1.1%) Tita. Macro. Lithos. .013 (17.1%)
	Iguano.	.039 (11.9%)		.035 (9.6%)		++
	Carnívora	.004 (18.4%)		.004 (18.5%)		++
Bipedals	Pros.	.009 (10.5%)	Plateos. .007 (10.9%) Sauropodi. .009 (10.8%)	.014 (16.3%)	Plateos. .015 (23.2%) Sauropodi. .013 (14.4%)	.043 (58.0%)
	Theropoda	.012 (6.4%)		.038 (20.2%)		.103 (52.6%)
	Metatheria*	.038 (9.8%)		.062 (15.7%)		++
Flyers	Aves	.045 (15.6%)	n. Pass. .036 (12.4%) Pass. .006 (6.9%)	.053 (18.1%)	n. Pass. .061 (20.8%) Pass. .006 (6.7%)	++
	Chiroptera	.013 (14.8%)	Megachi. .008 (11.9%) Microchi. .012 (14.3%)	.013 (15.4%)	Megachi. .012 (17.5%) Microchi. .011 (13.4%)	++
	Pterosauria	.018 (10.2%)	Rhampho. .019 (10.5%) Pteroda. .012 (10.7%)	.027 (15.7)	Rhampho. .028 (15.8%) Pteroda. .017 (16%)	++

Table 7.9 *clr* variance and variance percentages for humerus and femur proportions (6 bones analyzed) and balance B1 (fore vs. hind limb) variance. var H - *clr* humerus variance (from biplots 6 bones); var F - femur *clr* variance (from biplots 6 bones); B1 - balance B1 variance (from balances analyses). Sample size: Artiodactyla n=63; Perissodactyla n= 24; non-Passerines n=603; Passerines n=97; Megachiroptera n=33; Microchiroptera n=184; Rhamphorhynchoidea n=13; Pterodactyloidea n=11; Carnivora n=13; Plateosauria n=4; Sauropodiformes n=4; non-Eusauropoda and non-Neosauropoda n=5; Diplodocoidea n=3; basal Titanosauria, basal Macronaria and Lithostrotia n=8; Theropoda n=9; Iguanodontia n=10; Metatheria n=17. # - the Diplodocoidea included only two species; * - the Metatheria sample included specimens with metatarsal IV instead of metatarsal III of the remaining groups; ++ - not calculated. Abbreviations: Rhampho. – Rhamphorhynchoidea; Pteroda. – Pterodactyloidea; Megachi. - Megachiroptera; Microchi. - Microchiroptera; n. Pass. - non-Passerines; Pass. - Passerines; Tita. - basal Titanosauria; Macro. - basal Macronaria; Lithos. - Lithostrotia; Plateos. - Plateosauria; Sauropodi. - Sauropodiformes; Pros. - Prosauropoda; Iguano. - Iguanodontia.

- in flyers, the variability trends among the distinct groups are more complex to identify. Although the majority of the analyzed groups reveal distinct humerus and femur *clr* variances, consequently presenting high levels of morphological integration

between the two bones, Passerines and Microchiroptera reveal sub-identical percentages of variances in the humerus and femur. This should be subjected to future studies combining functional morphology and shape analysis.

The above cited inferences allowed speculating that the disparity of humerus and femur proportions seems to be more associated to locomotor function than to phylogeny.

Chapter 8 - Conclusions/Future Studies

"The cockroach and the birds were both here long before we were. Both could get along very well without us, although it is perhaps significant that of the two the cockroach would miss us more."

Joseph Wood Krutch, *The Twelve Seasons*, November pp. 118–19

Preamble

In an early stage of this thesis work, the compositional data analysis, as well as the exploration of disparity in morphospaces and the related macroevolutionary concepts of modularity and morphological integration constituted a single and reduced chapter in the thesis draft. The other chapters were to be constituted by the 3D sauropodomorphs data that I was acquiring around the world in order to perform Geometric Morphometric analyses on those materials, as well as on the dinosaur ichnological record. How far could my scientific naivety go!

After presenting an early work in the Morphofest 2006, in Vienna, Fred Bookstein told me that there was a mathematician working with different tools in Compositional Data - John Aitchison. Soon after, I was contacting Vera Pawlosky-Glahn at the Universidad of Girona, which, after kindly reading several of my e-mails, just answered “Come here to Girona and we will look at those dinosaurs of yours!” That was how and when the other alleged chapters of my thesis simply ended in the standing-by projects icebox …

Simultaneously, the never ending mixture of biological ideas and concepts in Angela Buscalioni’s mind just pushed me to combine this new approach in dealing with compositional data in its applicability for morphological integration, modularity or disparity.

“One of the chief charms of collecting is its uncertainty. One day you will go out loaded down with nets and bags for the sole purpose of catching bats, and you will arrive back in camp with a python in the nets, your bags full of birds, and your pockets full of giant millipedes.”

Gerald M. Durrell, *The Overloaded Ark*, p. 92

This chapter is divided into five parts, each of them summarizing some of the most relevant information generated by this study, as well as the issues yielding future studies. This chapter is little more than a brief resume of the “Final Remarks” included at the end of most chapters and sections, as follows:

8.1 **-** Compositional Data Analysis Methodology;

8.2 - Reanalyses; Bats/Pterosaurs/Birds;

8.3 - Sauropodomorpha;

8.4 - Dinosauria and Mammalia;

8.5 - Future Studies.

8.1 - Compositional Data Analysis methodology

As seen in previous chapters, when one has a biological or paleontological compositional problem, the interest lies in the relative magnitude and variations of components, rather than in their absolute values - this is achieved working with Compositional Data Analysis (CDA).

The CDA permitted a rigorous numerical approach to the characterization of biological and paleontological problems that deal with bone proportions. This improvements mainly allowed: a better quantification of compositions variation; quantification and discrimination of groups/areas within the morphospaces, as well as the associated occupation patterns; quantification of the morphospaces dissimilarities among and between groups; the introduction of a disparity index for proportions morphospaces - Aitchison Distance; the integration of size in proportions disparity analyses and the rationalization of how size is involved in the variation; the application of the CDA variables as numeric indicators in morphological integration and modularity studies; better information on morphological variation constrains in limb proportions morphospaces.

The biplots exploration techniques allow identifying and quantifying which are the parts with higher variation, as well as the relations between them. Moreover, the study of the bivariate correlations of A.D. and size and the analysis of biplots make it possible to establish an adequate and complementary understanding of the proportion variability patterns among the distinct groups of animals and the respective limb bone parts. The disparity and size analyses discriminate where and how size is influencing the bone proportions variation. The groups centroids position informs on the placement within the morphospace, whereby the groups disparity indexes A.D. (group intradistances) points to the distribution of specimens.

8.2 - Reanalyses; Bats/Pterosaurs/Birds

Applying the CDA methodology permitted the recognition that the linear trends referred in the archosaurs skull morphospace are not as evident as originally stated; the establishment of a correction in the identification of outliers in skull bone proportions; the introduction of a measure of morphological disparity, Aitchison Distance, which in turn allows a precise index of taxa comparison and specimens in proportions morphospaces; the identification of contrast variability patterns among the skull parts.

Bats, birds and pterosaurs: The consistent difference in proportions morphospaces patterning and distances of group centroids of pterosaurs to bats, both in fore and hind limbs, had never been previously quantified applying the adequate numerical methodologies. The results of regression analyses of *ilr* variable showed that size is only a significant factor for Megachiroptera, that is to say, there is a significant correlation between fore limb size and brachial index in Megachiroptera. The size of the hind limb is significantly correlated with balance B3 in several groups, namely positively correlated in both Aves groups (low correlation) and in Rhamphorhynchoidea pterosaurs, and being negatively correlated (low correlation) in Microchiroptera bats.

Chiroptera: in bats the fore limb is more conservative than the hind limb; Microchiroptera demonstrates higher fore limb proportions variability than Megachiroptera, which reveals higher hind limb variability than Microchiroptera; in Microchiroptera the variability steadily increases distally in the fore limb; in both groups the most variable bone is the metatarsal being this structure more variable in Megachiroptera than in Microchiroptera.

Pterosauria: in pterosaurs one observes an increase of variability from proximal to distal bones in the fore limb of both groups and in Pterodactyloidea there is a similar trend in the hind limb; there is an approximately constant ratio between femur and tibia in both groups of pterosaurs (0.75 for Rhamphorhynchoidea and 0.66 for Pterodactyloidea); Pterodactyloidea is more dissimilar among individuals in hind limb proportions than Rhamphorhynchoidea, which is more dissimilar in the fore limb; the humerus, femur and tibia reveal similar relative variance in both pterosaur groups; the autopodium bones are the biggest origin of variability although at different scales for the groups of pterosaurs; metacarpal and tibia are the elements that mostly contribute to the total variance of Rhamphorhynchoidea, while the major sources of variability among Pterodactyloidea are the metatarsal and metacarpal.

8.3 - Sauropodomorpha

The present work allowed to make some considerations on the proportions of non-adult sauropodomorphs. Juvenile sauropods have an opposite morphospace location to juvenile prosauropods, that is to say, in young developmental stages sauropods are close to the bipedal area of the morphospace. It can be speculated, though, that future ontogenetic analysis of limb proportions must be performed in order to evaluate probable appendicular heterochrony.

As an example of the unorthodox and dual mode of sauropodomorphs locomotion, one could refer that, despite presenting a big body mass, which could compel the attribution of a quadrupedal locomotion, the results of CDA concerning Sauropodiformes show that this group of prosauropods present both a fore limb and a hind limb proportions variation, in general, and humerus vs. femur variation, in particular, that classify it as bipedals. Nevertheless, one could state that the bipedal model of locomotion in prosauropods is somewhat distinct of others bipedals.

Both in fore and hind limbs morphospaces characteristic prosauropod and sauropod areas were detected, corresponding to “bipedal to facultative quadruped” and “quadruped”, respectively. Sauropods reveal a distinct cluster when compared to prosauropods, occupying a morphospace area resultant of higher femur and lower metatarsal proportions than the latter. Derived sauropods present wider patterns of exploration in hind limb morphospace and these patterns are related to size.

Some of the morphological differences between the two main groups of sauropodomorphs are more evident in the hind limb than in the fore limb. Both sauropodomorph groups hind limb variability is associated mainly with the metatarsal proportion and, at a minor scale, with the femur proportion in prosauropods, and with the tibia proportion in sauropods. As for the fore limb, both sauropodomorph groups variability is associated mostly with the metacarpal proportion and, at minor scale, with both humerus and radius proportions in prosauropods and with radius proportion in sauropods.

Evolutionary trends in Sauropods: There seem to be a general increase in intragroups fore limb variability along the clade, although not completely linear, since there is a reduction in basal Macronaria and basal Titanosauria. If one combines the individual groups, the general trend of variability increase among sauropods is fully confirmed. A general trend of reduction in fore limb intergroups A.D. is detected along

the clade, because groups that are phylogenetically closer have lower fore limb A.D. than do more phylogenetically distant groups.

Size is directly correlated with disparity in sauropods, with the exception of the most primitive and derived sauropod groups, thus implying that larger sauropods are more variable; size increase implied a wider occupation of hind limb morphospace; the femur and tibia proportions allow separating derived sauropods from other sauropods.

Evolutionary trends in Prosauropods: the hind limb among this clade is less variable than in sauropods, while the fore limb, in contrast, is more variable; the metatarsal is the divergent element within a general sauropodomorphs trend of increase in variability from proximal to distal bones; they are more conservative than sauropods regarding femur and tibia, while comparatively more disparate regarding humerus and radius; prosauropods femur proportion variance is equivalent to the tibia proportion variance while sauropods tibia variability is bigger than the femur variability; the fore limb is more variable than the hind limb and the variation is mainly detected in the metacarpal and in the radius parts.

Although the bivariate correlation signals of A.D. and size are not significant for prosauropods, it has been noticed that the small influence of size on fore limb disparity is divergent in Plateosauria and Sauropodiformes.

The statistical tests performed on the parts proportions (*ilr*) allow to state that there is a specific position for each group studied both in the fore limb as well as in the hind limb morphospaces, that is to say, each group occupies a precise area of the morphospace. Although the morphospace position of certain groups is different, its group occupation pattern could be identical, revealing this way similar specimens distribution for distinct clades.

8.4 - Dinosauria and Mammalia

One has detected that the morphological integration between fore and hind limbs is high in quadrupedals like sauropods, perissodactyls, artiodactyls and carnivores. This fact is corroborated by the equivalent variance in humerus and femur proportions showed by these quadrupedals.

Bipedals revealed low levels of morphological integration between limbs in theropods, prosauropods, non-Passerines, Megachiroptera and kangaroos. The low morphological integration among bipedals is corroborated by the distinct variance of humerus and femur proportions.

Full quadrupedal animals are, therefore, more conservative among limb proportions/variability than bipedal or facultative quadrupedal or even flying animals. The bipedal/facultative quadrupedal groups Plateosauria, Sauropodiformes, Aves, Pterosauria and Chiroptera exhibit, therefore, more variability when one deals with fore vs. hind limb elements and the humerus variability is considerable distinct from the femur variability.

Typical bipedals (e.g., theropods) are more distinguishable, when compared to quadrupedals (e.g., sauropods), in the hind limb morphospace than in the fore limb morphospace. In other words, in the hind limb morphospace there is a more evident gap area between the two modes of locomotion than in the fore limb morphospace. Corroborating this, a saurischian area within the fore limb morphospace was detected.

Metatheria, Artiodactyla, Perissoadctyla, Theropoda and non-Iguanodontia reveal a relationship of size and hind limb morphospace disparity identical to derived sauropods, except Lithostrotia.

Balance B1 results seem to indicate that, in prosauropods and theropods, both limbs are poorly integrated, that is to say, since there is high variation among limbs the morphological integration between fore and hind limbs is low. If this statement

is sufficient to classify the bipedal condition, or should be complemented with the comparative study of variances, should be a subject of future analyses.

8.5 - Future Studies

How are the limb bones proportioned?

This was the core question of the present work. As a result, and trying to solve the "why" question for the proportions, most of the results herein presented constitute a starting point or raw material for deeper functional and morphological analyses and methodological approaches.

To what extent this variation in proportion may affect the morphology should be explored in future studies in which the application of 3D geometric morphometrics will allow to improve the characterization of the morphological changes occurred in the evolutionary history of sauropodomorphs. This work is only in stand-by, since numerous sauropodomorph appendicular skeletons have already been digitized and the 3D data is available for analyses.

Theropods and the most derived group of sauropods reveal a low A.D. of 0.053. This fact is intriguing, since these two groups are separated both phylogenetically and functionally (theropods are bipedal, while the referred sauropods are quadrupedal). This A.D. similarity could be justified by the fact that, despite the absolute differences in length, both groups present similar proportions relationships among the three fore limb bones. Nonetheless, the closeness in the forelimb morphospace of these two different groups should be regarded more attentively in future studies, namely increasing the theropod sample.

If one considers the humerus-radius variability as an evolutionary novelty within Sauropodomorpha, one should expect the existence of a correlation between morphology and the proportions. Also, Sauropoda node could also be defined as the

one in which the variation pattern among the three parts of the hind limb is maximal in Sauropodomorpha. These facts open up future research fields.

As stated, the balance fore vs. hind limb could be employed to better discriminate prosauropods from sauropods. Previously considered of less importance, the balance femur and tibia vs. metatarsal also revealed to be an important source of information, and should also be employed in a future Discriminant Analysis study. Thus, the role of the hind limb proportions demands being analyzed in detail, since it was herein identified as an essential factor in the appendicular proportions differences among prosauropods and sauropods. The two modes of locomotion among these groups could be more deeply linked to the hind limb proportions than previously thought.

The exceptions to the condition of a flyer or bipedal having distinct humerus and femur variabilities, and consequently low morphological integration values, verified on Passerines birds and Microchiroptera bats, is another interesting evolutionary and functional question to be tested in the future.

The CDA allow to model missing values in order estimate, with numerical refinement, the absent osteological materials dimensions/proportions.

8 - Conclusões/Projectos-Estudos Futuros

"The cockroach and the birds were both here long before we were. Both could get along very well without us, although it is perhaps significant that of the two the cockroach would miss us more."

Joseph Wood Krutch, *The Twelve Seasons*, November pp. 118–19

Preâmbulo

A análise de dados composicionais, bem como a exploração da disparidade em morfoespaços e os conceitos macroevolutivos associados de modularidade e integração morfológica constituíam apenas um capítulo do então esboço de tese. Os capítulos restantes seriam compostos pela análise de morfometria geométrica dos dados 3D de Sauropodomorpha que me encontrava a digitalizar em vários museus do mundo, para além do mesmo tipo de análise no registo icnológico de dinossauros. Quanta ingenuidade científica!

Após apresentar um trabalho inicial em dados composicionais no Morphofest 2006, em Viena, Fred Bookstein advertiu-me para a existência de um matemático a trabalhar com um conjunto de técnicas novas em dados composicionais – John Aitchison. Pouco tempo depois, eu contactaria Vera Pawlosky-Glahn, da Universidad of Girona, que, após gentilmente ter lido vários e-mails meus, me respondia: "Vem até Girona para eu ver esses teus dinossauros!" E foi este o motivo pelo qual os outros alegados capítulos da minha tese se encontram (ainda) no limbo dos projectos científicos "em vias de".

Simultaneamente, a infindável amálgama de ideias e conceitos biológicos que constantemente fervilham na cabeça de Ángela Buscalioni, levou-me também a associar esta nova abordagem quantitativa no tratamento de dados composicionais e a sua aplicação a um contexto macroevolutivo, em integração morfológica, modularidade e disparidade.

"One of the chief charms of collecting is its uncertainty. One day you will go out loaded down with nets and bags for the sole purpose of catching bats, and you will arrive back in camp with a python in the nets, your bags full of birds, and your pockets full of giant millipedes."

Gerald M. Durrell, *The Overloaded Ark*, p. 92

Este capítulo encontra-se dividido em cinco partes, cada uma das quais resumindo a informação mais relevante gerada pelo presente estudo, bem como aspectos merecedores de futuros estudos e projectos de investigação. Assim, não é mais do que um breve resumo dos "Final Remarks" incluídos no final da maioria dos capítulos e secções, como tal consistindo em:

8.1 **–** Análise Composicional de Dados – metodologia;

8.2 – Reanálises; Morcegos/Pterossauros/Aves;

8.3 – Sauropodomorpha;

8.4 – Dinosauria e Mammalia;

8.5 – Projectos/Estudos Futuros.

8.1 Análise Composicional de Dados – metodologia

Tal como foi descrito nos capítulos anteriores, quando um problema biológico ou paleontológico envolve dados composicionais, a importância está mais na sua magnitude relativa e na variação das componentes, do que nos seus valores absolutos - esta aspiração é atingida utilizando a Análise de Dados Composicionais (CDA).

A CDA permite uma abordagem numérica rigorosa na caracterização de problemas biológicos e paleontológicos que impliquem a manipulação de proporções. Estes refinamentos permitem principalmente uma melhor quantificação da variação das composições; a quantificação e discriminação de grupos/áreas nos morfoespaços, bem como dos padrões de ocupação dos mesmos; a introdução de uma métrica/índice de disparidade em morfoespaços de proporções - Distância de Aitchison (A.D.); a incorporação da variável tamanho em análises de disparidade em proporções e de como o tamanho influencia a variabilidade; a aplicação de variáveis CDA como indicadores numéricos em estudos de integração morfológica e modularidade; e, por

fim, um melhor conhecimento das condicionantes da variabilidade morfológica em morfoespaços de proporções de esqueleto apendicular.

As técnicas exploratórias empregando *Biplots* permitiram identificar e quantificar quais as partes com maior variabilidade, bem como as relações entre elas.

Adicionalmente, o estudo de correlações entre A.D. e tamanho, a par da análise de *Biplots*, permitiram estabelecer um conhecimento adequado e complementar dos padrões de variabilidade de proporções entre os distintos grupos de animais analisados e as respectivas componentes do esqueleto apendicular. As análises da relação entre A.D. e tamanho discriminaram onde e como o tamanho está a influenciar a variabilidade de proporções. A posição dos centróides dos grupos é informativa quanto ao seu posicionamento no morfoespaço, enquanto os índices grupais de disparidade A.D. (distâncias intragrupo) remetem para a distribuição dos exemplares.

8.2 Reanálises; Morcegos/Pterossauros/Aves

A aplicação da metodologia CDA permitiu: o reconhecimento de que as tendências lineares referidas para o crânio de Archosauria não são tão evidentes como originalmente indicado (Marugán and Buscalioni 2003); o estabelecimento de correcções na identificação de *outliers* nas proporções do esqueleto craniano; a introdução de uma métrica de disparidade morfológica, A.D., a qual é um índice preciso na comparação de taxa e de exemplares em morfoespaços de proporções; a identificação de padrões contrastantes de variabilidade entre as componentes cranianas.

Morcegos/Pterossauros/Aves:

A diferença consistente na segmentação e distâncias entre centróides de pterossauros e morcegos, em morfoespaços de proporções e tanto nos membros

anteriores como nos posteriores, não havia sido anteriormente quantificada aplicando metodologias numéricas adequadas. Os resultados das regressões das variáveis *ilr* demonstraram que o tamanho é um factor significativo nos morcegos Megachiroptera, ou seja, existe uma correlação significativa entre o tamanho do membro anterior e o índice braquial neste grupo de morcegos. O tamanho do membro posterior está significativamente correlacionado com o *Balance* B3 tanto em Aves como nos pterossauros Rhamphorhynchoidea (baixa correlação) e está negativamente correlacionado nos morcegos Microchiroptera.

Chiroptera:

Nos morcegos, em termos de variabilidade de proporções, o membro anterior é mais conservador do que o membro posterior; Microchiroptera apresenta uma maior variabilidade nas proporções do membro anterior do que Megachiroptera, grupo que revela maior variabilidade no membro posterior; em Microchiroptera a variabilidade aumenta distalmente e de forma gradual no membro anterior; em ambos os grupos de morcegos o osso com maior variabilidade é o metatarso, revelando Megachiroptera maior variabilidade no metatarso do que Microchiroptera.

Pterosauria:

Em ambos os grupos de pterossauros é possível constatar um aumento da variabilidade dos ossos proximais para os distais, no membro anterior e uma tendência semelhante no membro posterior, em Pterodactyloidea; existe um ratio aproximadamente constante entre o fémur e a tíbia em ambos os grupos de pterossauros (0.75 para Rhamphorhynchoidea e 0.66 para Pterodactyloidea); Pterodactyloidea é mais dissimilar entre indivíduos nas proporções do membro posterior do que Rhamphorhynchoidea, grupo mais dissimilar no membro anterior; o úmero, fémur e tíbia revelam variâncias relativas semelhantes em ambos os grupos de pterossauros; o metacarpo e o metatarso são os elementos que contribuem

maioritariamente para a variabilidade dos grupos de pterossauros, apesar de em escalas distintas; o metacarpo e a tíbia são os elementos que mais contribuem para a variância total em Rhamphorhynchoidea, enquanto os elementos que mais contribuem para a variância total em Pterodactyloidea são o metacarpo e o metatarso.

8.3 Sauropodomorpha

O presente trabalho permitiu formular algumas considerações sobre as proporções do esqueleto apendicular em sauropodomorfos juvenis. Os saurópodes juvenis apresentam um posicionamento distinto do dos prossaurópodes, ou seja, em fases precoces do desenvolvimento os saurópodes localizam-se junto à área dos bípedes no morfoespaço de proporções. Pode-se especular, contudo, que análises ontogenéticas futuras em proporções do esqueleto apendicular devam ser realizadas com o objectivo de avaliar uma possível heterocronia apendicular.

Como exemplo da heterodoxia e modo dual de locomoção em sauropodomorfos pode referir-se que, em relação a Sauropodiformes, os resultados CDA revelaram que este grupo de prossaurópodes apresenta tanto a variabilidade entre membro anterior e posterior, em geral, como a variabilidade de úmero vs. fémur, em particular, típicas de bípedes. Contudo, os resultados deste trabalho revelaram que o modo de locomoção em prossaurópodes é algo distinto de outros bípedes.

Tanto em morfoespaços do membro anterior como do membro posterior foram detectadas áreas específicas para prossaurópodes e para saurópodes, correspondentes a “bípedes a quadrúpedes facultativos” e “quadrúpedes”, respectivamente. Os saurópodes revelaram um agrupamento distinto do dos prossaurópodes, ocupando os primeiros uma área do morfoespaço resultante de percentagens maiores de fémur e menores de metatarso, comparativamente aos segundos. Os saurópodes derivados revelaram padrões mais amplos de exploração

do morfoespaço do membro posterior, estando este padrão de disparidade correlacionado com o tamanho.

Algumas das diferenças morfológicas entre os dois grupos de sauropodomorfos são mais evidentes nas proporções do membro posterior do que nas do membro anterior. A variabilidade no membro posterior de ambos os grupos de sauropodomorfos está associada principalmente à proporção do metatarso e, em menor escala, à proporção do fémur em prossaurópodes e à proporção da tíbia em saurópodes. No que diz respeito ao membro anterior, a variabilidade nos grupos de sauropodomorfos está associada principalmente à proporção do metacarpo e, em menor escala, às proporções do úmero e do rádio em prossaurópodes e à proporção do rádio em saurópodes.

Tendências evolutivas em Saurópodes:

Este trabalho verificou que existe um aumento na variabilidade do membro anterior ao longo do clado Sauropoda, apesar de não complemente linear, já que se constatou uma redução em Macronaria basais e Titanosauria basais. Se combinarmos os grupos de saurópodes numa única amostra, a tendência de aumento de variabilidade ao longo do clado verifica-se plenamente. Verificou-se, também, uma redução nas distâncias A.D. intergrupos ao longo do clado Sauropoda no membro anterior, uma vez que grupos filogeneticamente próximos apresentam menores distâncias A.D. intergrupos do que grupos filogeneticamente mais afastados.

O tamanho está directamente correlacionado com a disparidade nos saurópodes, com a excepção dos saurópodes mais primitivos e dos mais derivados, implicando este facto que os saurópodes maiores apresentam maior variabilidade de proporções; o tamanho implicou uma ocupação mais ampla do morfoespaço do membro posterior; as proporções do fémur e da tíbia permitem discriminar os saurópodes mais derivados dos restantes saurópodes.

Tendências evolutivas em Prossaurópodes:

O membro posterior neste clado apresenta menor variabilidade do que em saurópodes, enquanto o membro anterior, pelo contrário, apresenta maior variabilidade; o metatarso é o elemento divergente na tendência genérica de aumento da variabilidade dos ossos proximais para os distais, verificada nos sauropodomorfos; os prossaurópodes são mais conservadores do que os saurópodes no que diz respeito às proporções do fémur e da tíbia, mas são mais díspares no que concerne às proporções do úmero e do rádio; a variância do fémur dos prossaurópodes é equivalente à da tíbia, enquanto a variabilidade da tíbia em saurópodes é maior do que a variabilidade do fémur; o membro anterior apresenta maior variabilidade do que o membro posterior e a maior variabilidade é detectada nas proporções do metacarpo e do rádio.

Apesar dos sinais das correlações entre A.D. e tamanho não serem significativos para prossaurópodes, foi detectado que a pequena influência do tamanho na disparidade do membro anterior é oposta em Plateosauria e Sauropodiformes.

Os testes estatísticos realizados utilizando *ilr* permitem afirmar que existe um posicionamento específico para cada grupo estudado, tanto paro o morfoespaço do membro anterior como para o morfoespaço do membro posterior, ou seja, cada grupo ocupa uma área específica dos morfoespaços.

Embora a posição nos morfoespaços de determinados grupos seja distinta, o seu padrão de ocupação do morfoespaço pode ser idêntico, revelando, desta forma, que clados distintos podem revelar padrões de distribuição idênticos nos morfoespaços.

8.4 Dinosauria e Mammalia

Foi detectado que a integração morfológica entre membro anterior e membro posterior é alta para os quadrúpedes, como saurópodes, perissodáctilos, artiodáctilos e carnívoros. Este facto é corroborado pelas variâncias equivalentes do úmero e do fémur destes grupos de quadrúpedes.

Os bípedes apresentam valores baixos de integração morfológica entre os membros anterior e posterior, nomeadamente em terópodes, prossaurópodes, aves não-Passerines, morecegos Megachiroptera e cangurus. Este facto é corroborado pelas variâncias distintas do úmero e do fémur destes grupos de bípedes.

Os animais quadrúpedes são, assim, mais conservadores nas proporções/variabilidade entre os dois membros do que os bípedes/quadrúpedes facultativos ou mesmo do que os voadores.

Os bípedes/quadrúpedes facultativos como Plateosauria, Sauropodiformes, ou voadores como Aves, Pterosauria e Chiroptera apresentam maior variabilidade quando se analisam as proporções dos elementos de membro anterior vs. membro posterior, tal como é significativo que a variabilidade do úmero seja consideravelmente diferente da variabilidade do fémur.

Bípedes típicos como os terópodes, por exemplo, discriminam-se melhor quando comparados com quadrúpedes, como por exemplo os saurópodes, no morfoespaço do membro posterior, do que no morfoespaço do membro posterior. Por outras palavras, no morfoespaço do membro posterior existe uma separação/área mais clara dos dois modos de locomoção do que no morfoespaço do membro anterior. Corroborando este facto, foi identificada uma área de Saurischia no morfoespaço do membro anterior.

Metatheria, Artiodactyla, Perissoadctyla, Theropoda e non-Iguanodontia apresentam relações entre tamanho e disparidade no morfoespaço do membro posterior idênticas às dos saurópodes derivados, à excepção de Lithostrotia.

Os resultados do *Balance* B1 indicam que, em prossaurópodes e terópodes, ambos os membros estão fracamente integrados, ou seja, uma vez que se verifica uma grande discrepância entre as variabilidades dos dois membros, a integração morfológica é baixa. Se esta premissa é suficiente para definir a condição bípede, ou se deve ser complementada com outros estudos comparativos de variância, deverá ser objecto de pesquisa futura.

8.5 Projectos/Estudos Futuros

Como estão os ossos do esqueleto apendicular proporcionados?

Esta foi uma questão chave ao longo deste trabalho. Como corolário, e tentando sempre resolver a questão "porquê" para as proporções, grande parte dos resultados aqui apresentados constituem um ponto da partida ou matéria-prima para o aprofundamento de análises funcionais ou morfológicas, bem como de outras abordagens metodológicas.

Em que medida a variabilidade nas proporções afecta a morfologia deverá ser explorado em futuros estudos, nos quais a aplicação de técnicas de morfometria geométrica 3D, sobre uma base de dados já construída, permitirá refinar a caracterização das modificações morfológicas ocorridas na história evolutiva dos sauropodomorfos. Este trabalho encontra-se actualmente em "reserva", já que vários esqueletos apendiculares do registo mundial de sauropodomorfos foram digitalizados em 3D.

Os terópodes e os saurópodes mais derivados apresentam uma A.D. baixa, sendo este facto intrigante, já que estes grupos estão afastados, tanto a nível filogenético, como a nível funcional. Este baixo valor de A.D. poderá ser justificado

pelo facto de, apesar das diferenças ao nível da tamanho absoluto, ambos os grupos poderem apresentar semelhanças ao nível das relações entre proporções das partes do membro anterior. Contudo, esta proximidade no morfoespaço do membro anterior destes dois grupos deverá ser encarado com maior atenção em estudos futuros, nomeadamente através do incremento da amostra de terópodes.

Se considerarmos a variabilidade úmero-rádio como um novidade evolutiva em Sauropodomorpha, deveremos esperar a existência de uma correlação entre a morfologia e as proporções. Da mesma forma, o nodo Sauropoda poderá ser definido como o nodo no qual o padrão de variabilidade entre as três partes do membro posterior é máximo em Sauropodomorpha. Estes factos abrem porta a novos campos de investigação.

Como já foi referido, o *balance* membro anterior vs. membro posterior pode ser utilizado para uma melhor discriminação entre prossaurópodes e saurópodes. Considerado anteriormente como de menor importância, o *balance* fémur e tíbia vs. metatarso revelou igualmente ser uma fonte de informação importante, podendo ser utilizado no futuro em estudos de Análise Discriminante.

Assim, o papel das proporções do membro posterior exige que estas sejam analisadas com maior profundidade, já que foram identificadas como um factor essencial nas diferenças das proporções do esqueleto apendicular entre prossaurópodes e saurópodes.

Os dois modos de locomoção destes dois grupos poderão estar mais profundamente ligados às proporções do membro posterior do que até agora se havia julgado.

As excepções à condição de um bípede ou voador apresentar distintas variabilidades no úmero e no fémur e, consequentemente, baixos valores de integração morfológica, verificadas nas aves Passerines e nos morcegos

Microchiroptera, constituem uma importante questão, quer a nível evolutivo, quer a nível funcional, que poderão ser testadas no futuro.

A CDA permitirá modelar os *missing values* com vista a estimar as dimensões/proporções dos materiais osteológicos não preservados.

8 - Conclusiones/Proyectos Futuros

"The cockroach and the birds were both here long before we were. Both could get along very well without us, although it is perhaps significant that of the two the cockroach would miss us more."

Joseph Wood Krutch, *The Twelve Seasons*, November pp. 118–19

Preámbulo

Los análisis de datos composicionales, así como la exploración de la disparidad a partir de la génesis de morfoespacios y de los conceptos macroevolutivos asociados a la modularidad e integración morfológica, constituían solo un capítulo del esbozo inicial de esta tesis. Los demás capítulos iban a desarrollar los análisis de morfometria geométrica de datos 3D de Sauropodomorpha a partir de los datos tomados digitalizando ejemplares en distintos Museos mundiales, conjuntamente con el mismo tipo de análisis para el registro icnológico de dinosaurios. Cuenta ingenuidad científica!

Después de presentar un trabajo preliminar en datos composicionales en el Morphofest 2006, en Viena, Fred Bookstein me informó que existiría un matemático trabajando con un nuevo conjunto de técnicas estadísticas aplicadas a datos composicionales. Poco tiempo después de eso, contacté con la Dra. Vera Pawlosky-Glahn de la Universidad de Girona que contestaría gentilmente a mis correos electónicos con: "Por que no vienes a Girona para que miremos esos dinosaurios!" Y ese fue el inicio de por qué los otros capítulos de mi proto-tesis todavía aguardan en el limbo de los proyectos…

Simultáneamente, el enorme conjunto de ideas y conceptos biológicos que Ángela D. Buscalioni tiene en su mente, me han conducido a combinar esta nueva aproximación metodológica de datos composicionales y su aplicación, con los contextos macroevolutivos relacionados con la integración morfológica, modularidad y disparidad.

"One of the chief charms of collecting is its uncertainty. One day you will go out loaded down with nets and bags for the sole purpose of catching bats, and you will arrive back in camp with a python in the nets, your bags full of birds, and your pockets full of giant millipedes."

Gerald M. Durrell, *The Overloaded Ark*, p. 92

Este capítulo se divide en cinco partes, y cada una de ellas resume la información más relevante generada en el presente estudio, así como algunos aspectos que deberán ser desarrollados en profundidad en estudios futuros. Este capítulo, además, es un resumen de las "consideraciones finales" contenidas en los capítulos de este estudio y en algunas secciones. Se estructura del siguiente modo:

8.1 **–** Análisis Composicionales de Datos – metodología;

8.2 – Reanálisis de morfoespacios ternarios: Murciélagos/Pterosaurios/Aves;

8.3 – Sauropodomorpha;

8.4 – Dinosauria y Mammalia;

8.5 – Proyectos Futuros.

8.1 - Análisis Composicionales de Datos – metodología

Tal como ha sido descrito en capítulos anteriores, cuando un problema biológico o paleontológico incluye datos composicionales, la importancia debería centrarse más en la magnitud relativa y en la variación de los componentes, que en los valores absolutos de los datos - objetivo del Análisis de Datos Composicionales (CDA).

El CDA permite una aproximación numérica y rigurosa en la caracterización de problemas biológicos y paleontológicos que impliquen la manipulación de proporciones, que habitualmente se han representado mediante diagramas ternarios. Estos refinamientos estadísticos permiten sobre todo: 1) una mejor cuantificación de la variación de las composiciones; 2) cuantificación y discriminación de grupos/áreas en morfoespacios, así como de sus patrones de ocupación - Distancia de Aitchison (A.D.); 3) la incorporación de la variable tamaño en análisis de la disparidad de proporciones, y de cómo el tamaño influye la variación; 4) aplicación de variables CDA como indicadores numéricos en estudios de integración morfológica y modularidad; 5) un

mejor conocimiento de los factores que condicionan la variabilidad morfológica en morfoespacios de proporciones, en este caso aplicado al esqueleto apendicular.

Así mismo la introducción de técnicas exploratorias empleando *biplots* permiten identificar y cuantificar las partes (elementos del esqueleto apendicular en este caso) con mayor variabilidad, así como la relación que existe entre ellas. Así pues cuando se anlizan conjuntamente el estudio de correlaciones entre A.D., el tamaño, y el análisis de *biplots* permiten establecer un marco adecuado para delimitar los patrones de variación que muestran los grupos de animales analizados en relación a cada uno de los componentes del esqueleto apendicular. Por una parte, los análisis de la relación entre A.D. y tamaño discriminan donde y como esta influyendo el tamaño en la variación de las proporciones. Por otra, la posición de los centroides de los grupos nos informa de la posición relativa que ocupan los grupos analizados en el morfoespacio, mientras los índices grupales de disparidad A.D. (intragrupo) remiten a la distribución de los ejemplares en el morfoespacio.

Con todo ello, esta metodología muestra un potencial extraordinario para caracterizar no sólo los diferentes aspectos relacionados con la variación de los componentes, sino con la propia ocupación de los grupos analizados en un morfoespacio empírico construido a partir de las proporciones. Las proporciones continen una fuente de información relevante para comprender un aspecto de la organización morfológica del fenotipo de los organismos.

8.2 – Reanálisis: Murciélagos/Pterosaurios/Aves

La aplicación de metodología CDA analizando casos publicados en la literatura científica donde se aplicaron análisis de proporciones representadas mediante diagramas ternarios permitió: 1) el reconocimiento de que las tendencias lineares citadas por ejemplo para el cráneo de Archosauria no son tan evidentes como originalmente fueron discutidas (Marugán y Buscalioni 2003); 2) la posibilidad de

corregir las proporciones y explorar la causas para el conjunto de *outliers* en del esqueleto craneal; 3) la introducción de una métrica de disparidad morfológica, A.D., la cual constituye un índice preciso en la comparación de *taxa* y de ejemplares en morfoespacios de proporciones; 4) la identificación de patrones de variación significativamente diferentes entre las componentes craneales.

Murciélagos/Pterosaurios/Aves:

El análisis de los componentes de la extremidad en amniotas voladores como murciélagos, pterosaurios y aves que no habían sido cuantificados anteriormente en trabajos previos aplicando metodologías numéricas adecuadas tanto en los miembros anteriores como en los posteriores, mostraron los siguientes resultados:

Utilizando las regresiones de las variables *ilr* se demuestra que el tamaño es un factor significativo en murciélagos Megachiroptera, o sea, que existe una correlación significativa entre el tamaño del miembro anterior y el índice braquial en este grupo de murciélagos. El tamaño del miembro posterior esta significativamente correlacionado con el *Balance* B3, tanto en Aves como en pterosaurios Rhamphorhynchoidea (baja correlación), y está negativamente correlacionado en los murciélagos Microchiroptera.

Chiroptera: en los murciélagos y en términos de variabilidad de proporciones, el miembro anterior es más conservador que el posterior. Microchiroptera presenta una variabilidad mayor en las proporciones del miembro anterior que Megachiroptera, grupo que es más variable en el miembro posterior. En Microchiroptera la variabilidad aumenta distalmente y de una manera gradual en el miembro anterior; en los dos grupos de murciélagos el hueso con variabilidad mayor es el metatarso, revelando Megachiroptera una mayor variabilidad en el metatarso que Microchiroptera.

Pterosauria: en ambos grupos de pterosaurios (Rhamphorhynchoidea y Pterodactyloidea) es posible verificar un aumento de la variabilidad de los huesos proximales en relación con los distales, en el miembro anterior. En Pterodactyloidea se

verifica una tendencia semejante para el miembro posterior. Existe un *ratio* aproximadamente constante entre el fémur y la tibia en ambos grupos de pterosaurios: 0.75 para Rhamphorhynchoidea y 0.66 para Pterodactyloidea. Pterodactyloidea es más disimilar entre individuos en las proporciones del miembro posterior que Rhamphorhynchoidea, que es un grupo que presenta mayor disimilitud en el miembro anterior. Húmero, fémur y tibia revelan variancias relativas semejantes en ambos grupos de pterosaurios. El metacarpo y el metatarso son los elementos que presentan mayor grado de variación en ambos grupos de pterosaurios, aunque a diferente escala. El metacarpo y la tibia son los elementos que más contribuyen para la variancia total en Rhamphorhynchoidea, mientras que en Pterodactyloidea son el metacarpo y el metatarso.

8.3 - Sauropodomorpha

Analizando las proporciones del 70% del registro de Sauropodomorpha con esqueleto apendicular, y constituyendo diferentes grupos atendiendo a las relaciones filogenéticas de Sauropodomorpha, se aplican los análisis CDA.

Tanto en morfoespacios del miembro anterior como del miembro posterior se detectaron áreas específicas para prosaurópodos y para sauropodos, correspondientes a “bípedos a cuadrúpedos facultativos” y “cuadrúpedos”, respectivamente. Los sauropodos revelan una asociación distinta cuando son comparados con prosaurópodos, ocupando un área del morfoespacio que resulta de porcentajes más grandes de fémur y menores de metatarso en los primeros que en los segundos.

Entre los resultados más relevantes se han realizado algunas consideraciones sobre las proporciones del esqueleto apendicular en sauropodomorfos juveniles. Los sauropodos juveniles presentan una posición distinta

en el morfoespacio, o sea, en fases precoces del desarrollo los sauropodos se localizan cerca de los bípedos prosaurópodos en el morfoespacio de proporciones. Se puede especular que análisis ontogenéticas futuras en proporciones del esqueleto apendicular deberán ser realizadas con el objetivo de evaluar una posible heterocronia apendicular.

Como ejemplo de la heterodoxia en el modo dual de la locomoción en sauropodomorfos, se puede referir que, en relación a Sauropodiformes, los resultados CDA revelaron que este grupo de prosaurópodos presentan tanto la variabilidad entre miembro anterior y posterior, en general, como la variabilidad de húmero vs. fémur, en particular, como típicos bípedos. Sin embargo, los resultados de este trabajo revelaron que el modo de locomoción en prosaurópodos es algo distinto al de otros bípedos.

Los sauropodos derivados mostraron patrones de exploración más amplios del morfoespacio para el miembro posterior, estando este patrón de disparidad correlacionado con el tamaño.

Algunas de las diferencias morfológicas entre los dos grupos de sauropodomorfos son más evidentes en las proporciones del miembro posterior que en las proporciones del miembro anterior. La variabilidad en el miembro posterior en los dos grupos esta asociada principalmente con la proporción del metatarso y, en menor escala, con la proporción del fémur en prosaurópodos, y con la proporción de la tibia, en sauropodos. En el miembro anterior, la variabilidad en sauropodomorfos esta asociada con la proporción del metacarpo y, a menor escala, con las proporciones del húmero y del radio en prosaurópodos, y con la proporción del radio en sauropodos.

Tendencias evolutivas en Sauropodos:

Este trabajo comprobó que existe un aumento general de la variabilidad del miembro anterior en el clado Sauropoda, mientras no totalmente linear, dado que se verificó una reducción en Macronaria basales y Titanosauria basales. Si uno reúne los

grupos de sauropodos en una sola muestra, la tendencia de aumento de variabilidad del clado Sauropoda es totalmente comprobada. Se verificó, también, una reducción de las distancias intergrupos A.D. en el clado Sauropoda y en el miembro anterior, dado los grupos filogenéticamente más cercanos presentan menores A.D. intergrupos que grupos filogeneticmente más lejanos.

El tamaño está directamente correlacionado con la disparidad en sauropodos, diferenciando a los sauropodos más primitivos de los más derivados, implicando este hecho que los sauropodos más grandes presentan una mayor variabilidad de proporciones. El tamaño implicó una ocupación más amplia del morfoespacio del miembro posterior; las proporciones del fémur y de la tibia permiten discriminar los sauropodos más derivados de los demás sauropodos.

Tendencias evolutivas en Prosaurópodos:

El miembro posterior de este clado presenta una variabilidad menor que en los sauropodos, mientras el miembro anterior, al revés, presenta una variabilidad mayor. El metatarso es el elemento divergente en la tendencia genérica de incremento en la variabilidad de los huesos proximales para los distales verificada en los sauropodomorfos. Los prosaurópodos son más conservadores que los saurópodos en lo que corresponde a las proporciones de fémur y de tibia, pero son más dispares en lo que corresponde a proporciones de húmero y de radio. La variancia de fémur de los prosaurópodos es equivalente a de la tibia mientras la variabilidad de la tibia en saurópodos es mayor do que la variabilidad del fémur. El miembro anterior presenta una variabilidad más grande que el miembro posterior y la mayor variabilidad se observa en las proporciones del metacarpo y del radio.

Aunque las señales de las correlaciones entre A.D. y tamaño no son significativas en prosaurópodos, se detectó una influencia pequeña del tamaño en la disparidad del miembro anterior que es opuesta en Plateosauria y Sauropodiformes.

Los test estadísticos realizados empleando *ilr* permiten afirmar que existe una posición especifica para cada grupo estudiado, tanto para el morfoespacio del miembro anterior como para el morfoespacio del miembro posterior, o sea, cada grupo ocupa una área especifica de los morfoespacios.

8.4 - Dinosauria y Mammalia

Incorporando en el estudio los datos sobre proporciones de un conjunto de mamíferos cuadrúpedos se explora la ocupación total del morfoespacio y se determinan cuestiones relacionadas con el tipo de locomoción en relación a los patrones de variación de los elementos en las extremidades anterior y posterior.

La integración morfológica entre miembro anterior y posterior es alta para los cuadrúpedos como saurópodos, perisodáctilos, artiodáctilos y carnívoros. Este dato es corroborado por las variancias equivalentes del húmero y del fémur de estos grupos de cuadrúpedos.

Los bípedos presentan valores bajos de integración morfológica entre los miembros anteriores y posteriores, sobre todo en terópodos, prosaurópodos, aves no-Passerines, Megachiroptera y canguros. Este dato se corrobora por las variancias diferentes de húmero y de fémur entre estos grupos de bípedos.

Los animales cuadrúpedos son, así, más conservadores en las proporciones/variabilidad entre los dos miembros que los bípedos/cuadrúpedos facultativos o que los voladores.

Los bípedos/cuadrúpedos facultativos y los voladores (Plateosauria, Sauropodiformes, Aves, Pterosauria y Chiroptera) presentan una variabilidad mayor cuando se analiza las proporciones de los elementos del miembro anterior vs. posterior, además la variabilidad del húmero es considerablemente diferente a la del fémur.

Bípedos típicos como terópodos, por ejemplo, se discriminan mejor cuando se enfrentan con cuadrúpedos, por ejemplo los saurópodos, en el morfoespacio del miembro posterior que en morfoespacio del miembro anterior. Por otras palabras, en el morfoespacio del miembro posterior existe una separación/área más distinta entre los dos tipos de locomoción que en el morfoespacio del miembro anterior.

Metatheria, Artiodactyla, Perissodactyla, Theropoda y non-Iguanodontia presentan relaciones entre tamaño y disparidad en el morfoespacio del miembro posterior idénticas a los saurópodos derivados, excepto a Lithostrotia.

Los resultados del *Balance* B1 indican que, en prosaurópodos y terópodos, los dos miembros están poco integrados, o sea, existe una gran discrepancia entre variabilidades de los dos miembros y la integración morfológica es baja.

8.5 - Proyectos Futuros

¿Como están proporcionados los huesos del esqueleto apendicular?

Esta fue la cuestión clave durante la realización de este trabajo. Los resultados aquí presentados constituyen un punto de partida para profundizar en la relación entre la morfología y su función. En este trabajo se muestra que los patrones de bipedia y cuadrupedia limitan de modo distinto los patrones de variación de los elementos que constituyen las extremidades y sus proporciones.

En que medida la variabilidad en las proporciones afecta la morfología deberá ser explorada en estudios futuros en los cuales la aplicación de técnicas de morfometria geométrica 3D, en una base de datos ya construida, permitirá refinar la caracterización de los cambios morfológicos ocurridos en la historia evolutiva de los sauropodomorfos. Este trabajo se encuentra actualmente en “reserva”, pues varios esqueletos apendiculares del registro mundial de sauropodomorfos ya fueron digitalizados en 3D.

Los terópodos y los saurópodos más derivados presentarán una A.D. intergroupo baja, constituyendo un facto curioso una vez que estos grupos están apartados tanto a nivel filogenético como funcional. Este bajo valor de A.D. podrá justificarse por el hecho de que, además de las diferencias al nivel de tamaño absoluto, ambos grupos puedan presentar semejanzas al nivel de relaciones entre proporciones de partes del miembro anterior. Sin embargo, esta proximidad en le morfoespacio del miembro anterior de estos dos grupos deberá ser mirada con más profundidad en estudios futuros, designadamente por el incremento de la muestra de terópodos.

Se consideramos la variabilidad húmero-radio como una novedad evolutiva en Sauropodomorpha, deberemos esperar la existencia de una correlación entre la morfología y las proporciones. Análogamente, el nodo Sauropoda podrá ser definido como el nodo en lo cual la variabilidad entre las tres partes del miembro posterior es máxima en Sauropodomorpha. Estos resultados abren la puerta para nuevos campos de investigación futura.

Como se refirió anteriormente, el *balance* miembro anterior vs. posterior puede ser empleado para una mejor discriminación entre prosaurópodos y saurópodos. Considerado anteriormente como de menor importancia, el *balance* fémur y tibia vs. metatarso reveló igualmente ser una fuente de información importante, pudiendo ser utilizado en estudios de análisis Discriminante.

Así, el papel de las proporciones del miembro posterior exige que estas sean analizadas con mayor profundidad, una vez que fueron identificadas como un factor esencial en las diferencias de las proporciones del esqueleto apendicular entre prosaurópodos y saurópodos.

Los dos tipos de locomoción de estos dos grupos podrán estar más profundamente conectados a las proporciones del miembro posterior do que hasta ahora se pensaba.

Las excepciones a la condición de que un bípedo o un volador presente distintas variabilidades en el húmero y en el fémur, y consecuentemente bajos valores de integración morfológica, que se verificaran en aves Passerines y en los murciélagos Microchiroptera, constituyen una importante cuestión, a nivel evolutivo y a nivel funcional, que deberán ser testadas en futuro.

El CDA permitirá calcular modelos para los *missing values* con el objetivo de estimar las dimensiones/proporciones en materiales osteológicos no preservados.

Chapter 9 – Literature cited

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Appendix 1 - Specimens List

"Every specimen is a permanent fact."

Plaque at entrance to the Earth History Hall, American Museum of Natural History

APPENDIX 1 - List of species; Groups; Institutional label; lengths (in milimeters) of humerus (H), radius (R), metacarpal III (MCIII), femur (F), tibia (T) and metatarsal III (MTIII); total fore limb length; total hind limb length; brachial index; intragroup A.D.; reference.

Institutional Abbreviations

AMNH, American Museum of Natural History, New York, USA;
BMNH, The Natural History Museum, London, UK formerly British Museum (Natural History);
CM, Carnegie Museum of Natural History, Pittsburgh, USA;
CDUTM, Chengdu University of Technology Museum, Chengdu, China;
CPL, Centro Paleontologico Los Barreales, Neuquén, Argentina;
IVPP, Institute of Vertebrate Palaeontology and Palaeoanthropology, Beijing, China;
FLMNH, Florida Museum of Natural History, USA;
FMNH, Field Museum of Natural History, Chicago, USA;
KAN Institute of Zoology, Kazak Academy of Sciences, Almaty, Kazakstan
KUVP, Museum of Natural History, University of Kansas, Lawrence, USA;
MACN, Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia', Buenos Aires, Argentina;
MB, Museum für Naturkunde der Humboldt-Universität zu Berlin, Berlin, Germany;
MCP, Museu de Ciências e Tecnologia, Pontifícia Universidade Catolica do Rio Grande do Sul, Porto Alegre, Brazil;
LDM, Lufeng Dinosaur Museum, Lufeng, China;
MCF-PVPH, Museo Municipal "Carmen Funes", Plaza Huincul, Neuquén, Argentina;
MHNM, Museum de Histoire Naturelle de Marrakeche, Marrakeche, Morocco;
MNHN, Muséum National d'Histoire Naturelle, Paris;
MLP, Facultad de Ciencias Naturales y Museo de La Plata, División Paleontología de Vertebrados, Buenos Aires, Argentina;
NM, National Museum, Bloemfontein, Free State, South Africa;
NSMT-PV, National Science Museum of Tokyo, Vertebrate Paleontology Collections, Tokyo;
PVL, Fundación Miguel Lillo, Universidad Nacional de Tucumán, San Miguel de Tucumán, Argentina;
SZ, University of Tübingen, Germany;
UCMP, University of California Museum of Paleontology, Berkeley, California;
UMMZ, University of Michigan Museum of Zoology, Ann Arbor, USA;
UNPSJB-PV, Universidad Nacional de la Patagonia ''San Juan Bosco''- Paleovertebrados, Comodoro Rivadavia, Argentina.
ZDM, Zigong Dinosaur Museum, Zigong, China
ZPAL, Institute of Paleobiology of the Polish Academy of Sciences in Warsaw, Poland;
YPM, Yale Peabody Museum, Yale University, New Haven, Connecticut;

6 bones												
Species	**Taxa**	**Label**	**H**	**R**	**MC III**	**F**	**T**	**MT III**	fore length	hind length	B.I.	Reference
Lufengosaurus magnus	Plateosauria	IVPP V.82	425	213	102	740	560	290	740	1590	1.9953	Young 1947
Lufengosaurus huenei	Plateosauria	IVPP V.15	335	190	80	580	395	225	605	1200	1.7632	pers. obs.
Plateosaurus engelhardi	Plateosauria	HMN Skelett VI	410	210	90	660	521	255	710	1436	1.9524	pers. obs.
Massospondylus carinatus	Plateosauria	BP/1/5347 A	9.82	6.47	2.16	11.33	10.6	4.9	18.45	26.83	1.5178	Reisz et al. 2005
Anchisaurus polyzelus	Sauropodiformes	YPM 1883	150	95	34	211	145	98	279	454	1.5789	Galton 1976
Gyposaurus sinensis	Sauropodiformes	IVPP V.43	133	72	20	237	183	102	225	522	1.8472	P. Upchurch pers. com. 2006 + Young 1948
Jingshanosaurus xinwaensis	Sauropodiformes	LV003	455	280	88	895	680	310	823	1885	1.6250	pers. obs. 2006
Yunnanosaurus huangi	Sauropodiformes	IVPP AS V.20	231	157	48	435	355	170	436	960	1.4713	pers. obs. 2006+ YOUNG 1942
Vulcanodon karibaensis	non-Eusauropoda	QG 24	700	647	206	1100	634	236	1553	1970	1.0819	Raath 1972 in Yates and Kitching 2003, table 1
Omeisaurus tianfuensis	non-Neosauropoda	ZDM T5701/500 5	1090	770	245	1310	860	230	2105	2400	1.4156	pers. obs.
Omeisaurus tianfuensis	non-Neosauropoda	IVPP T5704	1040	771	244	1271.5	869	180	2055	2320.5	1.3489	Carrano 1998a + I. Takejiri pers. com. 2007
Shunosaurus lii	non-Neosauropoda	ZDM T5402	670	480	170	1200	680	175	1320	2055	1.3958	pers. obs. + Zhang 1988
Mamenchisaurus guangyuanensis	non-Neosauropoda	CDUTM small specimen	455	297	120	640	410	115	872	1165	1.5320	pers. obs.
Apatosaurus louisae	Diplodocoidea	CM 3018	1150	800	293	1785	1115	236	2243	3136	1.4375	pers. obs.+ Gilmore 1936 + Bonnan 2001
Apatosaurus ajax	Diplodocoidea	NSMT-PV 20375	1033	616	309	1470	943	210	1958	2623	1.6769	Upchurch et al. 2004b
SMA 0009	Diplodocoidea	SMA 0009	181.6	134.1	45.3	224.8	186.5	44.5	361	455.8	1.3542	Schwarz et al. 2007
Bellusaurus sui	basal Macronaria	IVPP V.83003	365	240	80	480	280	92	685	852	1.5208	pers. obs.
Camarasaurus supremus	basal Macronaria	KUVP 129716	1120	745	348	1465	901	219	2213	2585	1.5034	Bonnan 2003 + Wilhite 2003
Bothriospondylus madagascariensis	basal Macronaria	****	1330	880	398	1460	870	230	2608	2560	1.5114	pers. obs. + Lapparent 1943
Epachthosaurus sciuttoi	basal Titanosauria	UNPSJB-PV 920	885	530	295	1095	700	177	1710	1972	1.6698	Martínez et al. 2004
Rapetosaurus krausei	Lithostrotia	FMNH PR 2209	438	324	184	594	500	89	946	1183	1.3519	Curry-Rogers pers. com. 2006
Laplatasaurus araukanicus	Lithostrotia	Av. 1046*	900	580	240	1000	650	225	1720	1875	1.5517	pers. obs. + Carrano 1998a + Huene 1929
Opisthocoelicaudia skarzynskii	Lithostrotia	ZPAL MgD I/48	1000	637	275	1395	810	200	1912	2405	1.5699	Carrano 1998b
Aeolosaurus rionegrinus	Lithostrotia	MPCA 27100	1035	580	295	1209	813	167	1910	2189	1.7845	Salgado et al. 1997b
Eoraptor lunensis	basal Theropoda	PVSJ 512	85	63	21	152	157	81	169	390	1.3492	T. Holtz pers. com. 2006
Herrerasaurus ischigualastensis	basal Theropoda	PVSJ 373	181.6	152	58	352	318	164.5	391.6	834.5	1.1947	Novas 1993 + Carrano 1998b
Acrocanthosaurus atokensis	Carnosauria	NCSM 14345	370	220	89	1277	960	439	679	2676	1.6818	Currie and Carpenter 2000
Dilophosaurus wetherilli	Ceratosauria	UCMP 37302	270	192	105	557	580	300	567	1437	1.4063	Holtz pers.com. 2006
Syntarsus rhodesiensis	Ceratosauria	QG 1	100	61	26	208	223	132	187	563	1.6393	Holtz pers.com. 2006
Albertosaurus libratus	Coelurosauria	UCMP 37302	324	156	98	1040	1000	594	578	2634	2.0769	Gatesy and Middleton 1997
Sinosauropteryx prima	Coelurosauria	NIGP 127586	22.5	12.5	7.5	53.2	61.2	40	42.5	154.4	1.8000	Currie and Chen 2001
Sinosauropteryx prima	Coelurosauria	NIGP 127587	40.9	22.2	14.3	86.4	96.8	62.5	77.4	245.7	1.8423	Currie and Chen 2001
Sinornithomimus dongi	Coelurosauria	IVPP−V11 797−10	212	145	53.8	323	335	213	410.8	871	1.4621	Kobayashi and Lü 2003
Hippopotamus amphibius	Artiodactyla	UMMZ 84041	350	245	125	465	280	115	720	860	1.4286	Gingerich 2003
Prosynthetoceras francisi	Artiodactyla	AM 32058	165	185	112	192	237	126	462	555	0.8919	Webb et al. 2003
Equus onager	Artiodactyla	****	222.6	291	207.9	303	297	243	721.5	843	0.7649	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Equus caballus przewalski	Artiodactyla	****	241.5	296	213.7	315.5	290.4	251	751.2	856.9	0.8159	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Camelus bactrianus	Artiodactyla	****	361	442	321	482	382	322	1124	1186	0.8167	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Tragulus meminna	Artiodactyla	****	76.1	60.3	37.9	99.05	103	58.9	174.3	260.95	1.2620	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Tragulus napu	Artiodactyla	****	66.6	61.9	42.2	87.9	96	54.5	170.7	238.4	1.0759	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Tragulus javanicus	Artiodactyla	****	68.2	55	35.95	84.5	91.45	54.1	159.15	230.05	1.2400	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Tragulus sp.	Artiodactyla	****	68.7	60.9	42.6	87.9	95	61.9	172.2	244.8	1.1281	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Okapi johnstoni	Artiodactyla	****	305	362.5	304	321.5	327	318	971.5	966.5	0.8414	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Giraffa camelopardalis	Artiodactyla	****	483	795	720	530	601	739	1998	1870	0.6075	K.E. Lilje pers.com. 2006 + Lilje et al. 2003

Tragelaphus spekei	Artiodactyla	****	215.6	218.1	202.6	278	313	217.2	636.3	808.2	0.9885	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Tragelaphus strepsiceros	Artiodactyla	****	248.5	291	284	322.5	347	285	823.5	954.5	0.8540	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Tragelaphus eurycerus	Artiodactyla	****	252	250.5	204	343	336.5	221	706.5	900.5	1.0060	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Boselaphus tragocamdus	Artiodactyla	****	247.5	299	252	324.5	339	251	798.5	914.5	0.8278	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Bubalus bubalis	Artiodactyla	****	286.5	300	225	376	344	240.5	811.5	960.5	0.9550	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Bison bison	Artiodactyla	****	266	301.5	182	337	320	225.5	749.5	882.5	0.8823	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Bison bonasus	Artiodactyla	****	322	345	216	426	421	262	883	1109	0.9333	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Cephalophus sylvicultor	Artiodactyla	****	188.5	183	158	252.5	238	171	529.5	661.5	1.0301	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Cephalophus dorsalis	Artiodactyla	****	110.9	106.2	89.9	152.9	142.1	105.4	307	400.4	1.0443	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Kobus ellipsiprymnus	Artiodactyla	****	220	247.5	223	307	314.5	217	690.5	838.5	0.8889	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Kobus leche	Artiodactyla	****	173.7	202.3	202.7	248.1	280.3	212.7	578.7	741.1	0.8586	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Pelea capreolus	Artiodactyla	****	129.5	171	180	177	226.5	185	480.5	588.5	0.7573	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Hippotragus niger	Artiodactyla	****	244	308.5	240	305	326	236	792.5	867	0.7909	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Oryx gazella	Artiodactyla	****	217.8	281.3	216.4	284.5	300.3	228.8	715.5	813.6	0.7743	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Addax nasomaculata	Artiodactyla	****	193	250	188	248.5	278	213.5	631	740	0.7720	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Damaliskus dorcas phillipsi	Artiodactyla	****	167	235	207	215	252.5	213.5	609	681	0.7106	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Alcephalus buselaphus	Artiodactyla	****	216.5	310	265	275	336	272.5	791.5	883.5	0.6984	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Connochaetes gnou	Artiodactyla	****	211.5	275	196	257	300	216	682.5	773	0.7691	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Oreotragus oreotragus	Artiodactyla	****	105.55	91.25	76	126.6	140	80.7	272.8	347.3	1.1567	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Raphicerus campestris	Artiodactyla	****	109.5	130	135	151.5	196	145	374.5	492.5	0.8423	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Madoqua saltiana	Artiodactyla	****	73.75	83.75	81.5	97.5	126.8	96.7	239	321	0.8806	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Madoqua guentheri	Artiodactyla	****	69.7	86	87.3	92	127.3	98.1	243	317.4	0.8105	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Aepyceros melampus	Artiodactyla	****	165	226	231	218.5	274	238	622	730.5	0.7301	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Aepyceros melampus	Artiodactyla	****	157.5	215	224.5	213.5	268	232	597	713.5	0.7326	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Litocranius walleri	Artiodactyla	****	155	205.5	261	194	249.5	225	621.5	668.5	0.7543	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Litocranius walleri sclateri	Artiodactyla	****	148.5	193	239	182.5	233	209	580.5	624.5	0.7694	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Gazella thomsoni	Artiodactyla	****	115.3	148.2	165	161.6	201.3	167.9	428.5	530.8	0.7780	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Gazella dama	Artiodactyla	****	176	246.5	268	226	289	271	690.5	786	0.7140	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Gazella dama mhorr	Artiodactyla	****	178	256	270	230	285	270	704	785	0.6953	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Saiga tatarica	Artiodactyla	****	129.7	162.8	149.6	166.5	189.3	164.1	442.1	519.9	0.7967	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Capricornis crispus	Artiodactyla	****	178	178.5	130	212	244.5	139.5	486.5	596	0.9972	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Rupicapra rupicapra	Artiodactyla	****	175.5	194	147.5	211.5	266	163	517	640.5	0.9046	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Rupicapra ruficeps	Artiodactyla	****	172	189	147	203	261	165.5	508	629.5	0.9101	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Capra ibex cylindricornis	Artiodactyla	****	188.5	203	133.5	236.5	272.5	136	525	645	0.9286	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Capra ibex	Artiodactyla	****	200.5	204.5	141	242	288	146	546	676	0.9804	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Capra pyrenaica	Artiodactyla	****	181	191.5	135.5	227	260.5	146.5	508	634	0.9452	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Capra hircus thibethanus	Artiodactyla	****	166.5	169.5	111.5	196	223.5	117	447.5	536.5	0.9823	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Ammotragus lervia	Artiodactyla	****	202.5	223	154	252	272	159	579.5	683	0.9081	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Ovis ammon orientalis	Artiodactyla	****	144	167.5	146	192	223	153	457.5	568	0.8597	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Ovis canadensis	Artiodactyla	****	196.2	233.1	195.5	263.5	308	210.2	624.8	781.7	0.8417	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Moschus moschiferus	Artiodactyla	****	141	146	139	184	225.5	175	426	584.5	0.9658	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Muntiacus reevesi	Artiodactyla	****	102.7	95.1	80	133.9	140.6	107.5	277.8	382	1.0799	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Muntiacus muntjac	Artiodactyla	****	121.5	114	101	158.5	171	127	336.5	456.5	1.0658	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Dama dama	Artiodactyla	****	207.5	235	216	273	311.5	248	658.5	832.5	0.8830	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Axis axis	Artiodactyla	****	156.5	169	156.5	207	234.5	171	482	612.5	0.9260	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Axis porcinus	Artiodactyla	****	133.3	128.5	114.5	183.5	197	135	376.3	515.5	1.0374	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Cervus unicolor	Artiodactyla	****	220.1	226.2	213.1	295.2	294.6	237.5	659.4	827.3	0.9730	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Cervus nippon	Artiodactyla	****	175	187.5	184.5	220.5	257	211	547	688.5	0.9333	K.E. Lilje pers.com. 2006 + Lilje et al. 2003

Cervus elaphus	Artiodactyla	****	241.8	287.4	242	312.5	316	244.5	771.2	873	0.8413	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Pudu pudu	Artiodactyla	****	101.2	81.7	55.2	124.5	127	79.1	238.1	330.6	1.2387	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Alces alces	Artiodactyla	****	374	414	343	420.5	474.5	398	1131	1293	0.9034	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Capreolus capreolus	Artiodactyla	****	138.5	159	151	178.5	223.5	182	448.5	584	0.8711	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Tapirus terrestris	Perissodactyla	UMMZ 160907	245	205	112.5	310	235	113.5	562.5	658.5	1.1951	Gingerich 2003
Tapirus bairdii	Perissodactyla	UMMZ 81051	250	215	109	325	245	113	574	683	1.1628	Gingerich 2003
Tapirus indicus	Perissodactyla	L-85.808	255	215	120	327	260	118	590	705	1.1860	Gingerich 2003
Hexaprotodon liberiensis	Perissodactyla	L-1952.4.1.4 /1914.6.21 .1	216.5	152.5	86.5	277.5	190	78.3	455.5	545.8	1.4197	Gingerich 2003
Aktautitan hippopotamopus	Perissodactyla	KAN N2/875 + N2/873	440	280	124	510	350	107	844	967	1.5714	Mihlbachler et al. 2004
Tapirus indicus	Perissodactyla	****	250	228	120	320	258	120	598	698	1.0965	Mihlbachler et al. 2004
Palaeosyops paludosis	Perissodactyla	AMNH 11689	293	228	109	355	285	111	630	751	1.2851	Mihlbachler et al. 2004
Dolichorhinus hyognathus	Perissodactyla	CM 11071	340	328	128	457	335	132	796	924	1.0366	Mihlbachler et al. 2004
Rhinotitan mongoliensis	Perissodactyla	IVPP V3254	497	480	205	685	465	198	1182	1348	1.0354	Mihlbachler et al. 2004
Brontops robustus	Perissodactyla	YPM 12048	608	504	230	812	448	200	1342	1460	1.2063	Mihlbachler et al. 2004
Hyrachyus agrarius	Perissodactyla	AMNH 5065	197	197	93	254	243	110	487	607	1.0000	Mihlbachler et al. 2004
Hyracodon nebrascensis	Perissodactyla	****	202	210	114	267	220	114	526	601	0.9619	Mihlbachler et al. 2004
Metamynodon planifrons	Perissodactyla	AMNH 546	393	320	153	480	280	118	866	878	1.2281	Mihlbachler et al. 2004
Menoceras arikarense	Perissodactyla	AMNH (Agate Springs)	244	253	136	327	290	128	633	745	0.9644	Mihlbachler et al. 2004
Chilotherium anderssoni	Perissodactyla	****	349	280	127	430	278	110	756	818	1.2464	Mihlbachler et al. 2004
Aphelops malacorhinus	Perissodactyla	FLMNH (Love Bone Bed)	384	345	178	476	343	143	907	962	1.1130	Mihlbachler et al. 2004
Teleoceras proterum	Perissodactyla	AMNH (Mixson's Bone Bed)	310	240	106	415	202	89	656	706	1.2917	Mihlbachler et al. 2004
Dicerorhinus sumatrensis	Perissodactyla	NMNH 49561	330	275	165	478	282	142	770	902	1.2000	Mihlbachler et al. 2004
Rhinoceros sondiacus	Perissodactyla	NMNH 269392	352	289	160	426	285	135	801	846	1.2180	Mihlbachler et al. 2004
Rhinoceros unicornis	Perissodactyla	NMNH 269392	405	340	215	520	341	177	960	1038	1.1912	Mihlbachler et al. 2004
Diceros bicornis	Perissodactyla	NMNH 162935	373	392	183	464	330	163	948	957	0.9515	Mihlbachler et al. 2004
Ceratotherium simum	Perissodactyla	NMNH 164635	407	375	196	520	354	171	978	1045	1.0853	Mihlbachler et al. 2004
Hexaprotodon liberiensis	Perissodactyla	NMNH 581892	219	156	88	277	200	78	463	555	1.4038	Mihlbachler et al. 2005
Toxodon burmeisteri	Perissodactyla	AMNH 14943	387	298	147	577	325	101	832	1003	1.2987	Mihlbachler et al. 2006
Acinonyx jubatus	Carnivora	SZ 3797	240.5	240	82	266	268.5	107	562.5	641.5	##	Schmieder 2000
Acinonyx jubatus	Carnivora	M. 202	194	195	75.5	216	222	96.5	464.5	534.5	##	Schmieder 2000
Panthera tigris	Carnivora	SZ 3769	311.5	251.5	106	351	294	122	669	767	##	Schmieder 2000
Panthera tigris	Carnivora	SZ 3728	326	274	111	364	321	128	711	813	##	Schmieder 2000
Panthera pardus	Carnivora	SZ 4227	228	184	80.2	248.5	238	96.9	492.2	583.4	##	Schmieder 2000
Panthera pardus	Carnivora	M. 203	207	175	72.1	237.5	217	87.6	454.1	542.1	##	Schmieder 2000
Panthera pardus	Carnivora	SZ 7301	239	201	82.5	260	242	93	522.5	595	##	Schmieder 2000
Panthera leo	Carnivora	SZ 3280	315.5	283	108.9	350	298.5	125.9	707.4	774.4	##	Schmieder 2000
Panthera leo	Carnivora	SZ 7497	345	308	122	373	326	132	775	831	##	Schmieder 2000
Panthera onca	Carnivora	Mam. 199	221	181	72.5	244	212	87.7	474.5	543.7	##	Schmieder 2000
Felis concolor	Carnivora	Mam. 198	185	153	67.6	223.5	197	84.7	405.6	505.2	##	Schmieder 2000
Smilodon fatalis	Carnivora	GPI, Tübingen	327	258	83	356	270	94.5	668	720.5	##	Schmieder 2000
Canis lupus	Carnivora	Mam. 190	196	199.5	88.5	213.5	219	94.1	484	526.6	##	Schmieder 2000
Isodon obesulus	Metatheria	M6560	48.5	40.3	13.4	73.4	72.9	23.4	102.2	169.7	##	N. Milne pers. com. 2006
Parameles gunnii	Metatheria	M16590	45.3	43.8	11.6	66.5	72.1	31.2	100.7	169.8	##	N. Milne pers. com. 2007
Macrotis lagotis	Metatheria	M16102	50.9	53.9	19	72.5	97.4	53.9	123.8	223.8	##	N. Milne pers. com. 2008
Phascolactus cinereus	Metatheria	M7953	129.6	140.7	36.8	165	128.4	33	307.1	326.4	##	N. Milne pers. com. 2009
Lasiorhinus latifrons	Metatheria	M924	112.7	103.5	22.8	140.7	114.6	24.2	239	279.5	##	N. Milne pers. com. 2010
Bettongia lesueur	Metatheria	M19074	31.8	35.4	8.5	68.8	85.2	35.2	75.7	189.2	##	N. Milne pers. com. 2011

Dendrolagus matschei	Metatheria	M2252	98.9	97.7	22.9	124.8	124.8	37.4	219.5	287	##	N. Milne pers. com. 2012
Lagorchestes conspicillatus	Metatheria	M6733	43.1	57.8	9.4	114.6	151	67.7	110.3	333.3	##	N. Milne pers. com. 2013
Macropus agilis	Metatheria	M11640	86.4	117.6	19.8	170	250	96.7	223.8	516.7	##	N. Milne pers. com. 2014
Macropus eugenii	Metatheria	M6573	56.9	74	12.5	108.9	162	58	143.4	328.9	##	N. Milne pers. com. 2015
Macropus fuliginosus	Metatheria	M16203	108.5	146.3	26.9	212	279.5	147.6	281.7	639.1	##	N. Milne pers. com. 2016
Petrogale brachiotis	Metatheria	M198880	51.2	62.4	11	118.1	140.3	48.6	124.6	307	##	N. Milne pers. com. 2017
Setonis brachiotus	Metatheria	M51202	50.7	62.2	13.1	107.8	117.2	41.1	126	266.1	##	N. Milne pers. com. 2018
Thylogale sp	Metatheria	M16211	70.6	85.6	14.4	135.9	174.4	55.1	170.6	365.4	##	N. Milne pers. com. 2019
Phalanger maculatus	Metatheria	M19077	70.2	70.3	14.7	88.1	77.7	18.4	155.2	184.2	##	N. Milne pers. com. 2020
Tricosurus vulpecula	Metatheria	M10906	68.6	76.4	14.4	87.8	88.5	18.8	159.4	195.1	##	N. Milne pers. com. 2021
Wyulda squamicaudata	Metatheria	M23221	50.6	51.5	11	75.6	66.3	14	113.1	155.9	##	N. Milne pers. com. 2022

Hind limb									
Species	**Taxa**	**Label**	**Intragroup A.D.**	**F**	**T**	**MT**	hind length	**Log hind**	**Reference**
Silesaurus opolensis	Dinosauromorpha	ZPAL Ab III/361/23	0.2506	198	170	77	445	2.6484	Dzik 2003
Lagosuchus talampayensis	Dinosauromorpha	UPLR 09	0.0566	40.6	46.6	24.1	111.3	2.0465	Carrano 1998a
Marasuchus lilloensis	Dinosauromorpha	PVL 3871	0.1769	57.5	70	40.4	167.9	2.2251	Sereno and Arcucci 1995
Marasuchus lilloensis	Dinosauromorpha	PVL 3870	0.1364	42.2	50.1	28	120.3	2.0803	Sereno and Arcucci 1996
Lagerpeton chanarensis	Dinosauromorpha	UPLR 06	0.0542	77.8	92.5	44	214.3	2.3310	Sereno and Arcucci 1993
Lagerpeton chanarensis	Dinosauromorpha	PVL 4619	0.0509	76.7	90	42.1	208.8	2.3197	Sereno and Arcucci 1993
Guaibasaurus candelariensis	Dinosauromorpha	MCN-PV 2355	0.1489	214	212	95	521	2.7168	Bonaparte et al. 1999
Thecodontosaurus caducus	basal Sauropodomorphs	BMNH P77/1	0.0702	72	70	35	177	2.2480	pers. obs. + Yates 2003a
Saturnalia tupiniquim	basal Sauropodomorphs	MCP 3844-PV	0.1144	152	158	84	394	2.5955	Langer 2003
Thecodontosaurus caducus	basal Sauropodomorphs	****	0.1667	255	180	110	545	2.7364	Heerden 1997, table 19.1
Plateosaurus sp.	Plateosauria	SMNS (F).10 (Doppelskelett 2)	0.0411	581	472	235	1288	3.1099	Carrano 1998a
Plateosaurus sp.	Plateosauria	SMNS (F).10 (Doppelskelett 1)	0.0216	718.5	590	275	1583.5	3.1996	Carrano 1998a
Plateosaurus engelhardi	Plateosauria	HMN Skelett 25	0.0868	550	482	200.6	1232.6	3.0908	pers. obs.+ Carrano 1998a
Plateosaurus engelhardi	Plateosauria	HMN Skelett 1	0.0964	628	527	220	1375	3.1383	Carrano 1998a
Plateosaurus engelhardi	Plateosauria	SMNS 13200	0.1002	680	500	240	1420	3.1523	Von Huene 1926 in Yates and Kitching 2003, table 1
Plateosaurus sp.	Plateosauria	AMNH 2106	0.1107	610	550	221	1381	3.1402	Carrano 1998a
Riojasaurus incertus	Plateosauria	PVL 3526	0.0697	461	377.5	195	1033.5	3.0143	pers. obs.+ Carrano 1998a
Riojasaurus incertus	Plateosauria	PVL 3808	0.0609	608	520	225	1353	3.1313	pers. obs.+ Carrano 1998a
Sellosaurus gracilis	Plateosauria	SMNS 12843	0.0510	551	458	230	1239	3.0931	Carrano 1998a
Lufengosaurus magnus	Plateosauria	IVPP V.82	0.0820	740	560	290	1590	3.2014	Young 1947
Massospondylus carinatus	Plateosauria	BMNH R.8171(QG 1159)	0.0168	360	295	140	795	2.9004	pers. obs.
Massospondylus sp.	Plateosauria	PVSJ juvenile	0.0758	220	199	96.2	515.2	2.7120	Carrano 1998a
Sellosaurus gracilis	Plateosauria	YPM 2192	0.2774	226	216	131	573	2.7582	Galton 1973
Sellosaurus gracilis	Plateosauria	SMNS 12354c	0.0741	480	420	177.8	1077.8	3.0325	Carrano 1998a
Sellosaurus gracilis	Plateosauria	SMNS 11838	0.1725	492	510	194	1196	3.0777	Carrano 1998a
Sellosaurus gracilis	Plateosauria	SMNS 17928	0.0477	491	428.5	207	1126.5	3.0517	Carrano 1998a
Plateosaurus engelhardi	Plateosauria	****	0.0553	987	790	360	2137	3.3298	Raath 1972
Plateosaurus robustus	Plateosauria	****	0.1481	900	650	290	1840	3.2648	Raath 1972
Lufengosaurus huenei	Plateosauria	IVPP V.15	0.1642	580	395	225	1200	3.0792	pers. obs.
Coloradisaurus brevis	Plateosauria	PVL_5904	0.0607	505	455	215	1175	3.0700	pers. obs.
Plateosaurus engelhardi	Plateosauria	HMN Skelett VI	0.0440	660	521	255	1436	3.1572	pers. obs.
Massospondylus carinatus	Plateosauria	BP/1/5347A	0.0831	11.33	10.6	4.9	26.83	1.4286	Reisz et al. 2005
Ammosaurus major	Sauropodiformes	YPM 209	0.0827	99	93	44.2	236.2	2.3733	Carrano 1998a

Ammosaurus major	Sauropodiformes	YPM 208	0.2573	221	260	120.7	601.7	2.7794	Carrano 1998a
Anchisaurus polyzelus	Sauropodiformes	YPM 1883 (YPM 2128)	0.2338	211	145	98	454	2.6571	Galton 1976
Gyposaurus sinensis	Sauropodiformes	IVPP V.43	0.0965	237	183	102	522	2.7177	P. Upchurch pers. com. 2006 + Young 1948
Gyposaurus sinensis	Sauropodiformes	IVPP V.27	0.3141	235.5	202	143	580.5	2.7638	Carrano 1998a
Jingshanosaurus xinwaensis	Sauropodiformes	LV003	0.1189	895	680	310	1885	3.2753	pers. obs.
Mussaurus patagonicus	Sauropodiformes	PVL 4068	0.0478	30	26.9	12.9	69.8	1.8439	Bonaparte and Vince 1979
Yunnanosaurus huangi	Sauropodiformes	IVPP AS V.20	0.0331	435	355	170	960	2.9823	pers. obs. + Young 1942
Euskelosaurus browni	Sauropodiformes	"Maphutseng Euskelosaurus"	0.5972	780	584	146	1510	3.1790	Raath 1972, table 9
Vulcanodon karibaensis	non-Eusauropoda	QG 24	0.1057	1100	634	236	1970	3.2945	Raath 1972 in Yates and Kitching 2003, table 1
Blikanasaurus cromptoni	non-Eusauropoda	SAM K403	0.1216	520	376	137	1033	3.0141	Carrano 1998b + (femur - estimated) Galton and Heerden 1998 in Yates 2004
Antetonitrus ingenipes	non-Eusauropoda	BP/1/4952	0.1061	794	512	197	1503	3.1770	Zhang (1988) in Yates and Kitching (2003)
Gongxianosaurus shibeiensis	non-Eusauropoda	****	0.2491	1213	882	209.5	2304.5	3.3626	He et al. 1998
Cetiosaurus mogrebiensis	non-Neosauropoda	****	0.2214	1850	1010	400	3260	3.5132	Carrano 1998a
Klamelisaurus gobiensis	non-Neosauropoda	IVPP V.9492	0.1896	1200	740	270	2210	3.3444	Carrano 1998a
Omeisaurus tianfuensis	non-Neosauropoda	ZDM T5701/5005	0.0639	1310	860	230	2400	3.3802	pers. obs. + He et al. 1988 in Yates and Kitching 2003; Guangzhao 2005, p.219
Omeisaurus tianfuensis	non-Neosauropoda	IVPP T5704	0.2441	1271.5	869	180	2320.5	3.3656	Carrano 1998a + Ike Takejiri pers. communic.
Shunosaurus lii	non-Neosauropoda	ZDM T5402	0.1405	1200	680	175	2055	3.3128	pers. obs. + Zhang 1988
Jobaria tiguidensis	non-Neosauropoda	MNN TIG3	0.0461	1800	1080	300	3180	3.5024	Sereno et al. 1999
Mamenchisaurus hochuanensis	non-Neosauropoda	CDUTM 02545	0.0483	1400	865	265	2530	3.4031	pers. obs.
Mamenchisaurus guangyuanensis	non-Neosauropoda	CDUTM small specimen	0.0350	640	410	115	1165	3.0663	pers. obs.
Apatosaurus louisae	Diplodocoidea	CM 3018	0.1612	1785	1115	236	3136	3.4964	pers. obs.+ Gilmore 1936 + Wilson and Upchurch 2003 + Bonnan 2001
Diplodocus carnegii	Diplodocoidea	CM 94	0.1042	1470	1006	215	2691	3.4299	pers. obs. + Carrano 1998a + Bonnan 2001
Diplodocus sp.	Diplodocoidea	****	0.3768	1430	1060	390	2880	3.4594	Carrano 1998a
Limaysaurus tessonei	Diplodocoidea	MUCPv-205	0.1325	1440	850	200	2490	3.3962	Carrano 1998a
Apatosaurus ajax	Diplodocoidea	NSM-PV 20375	0.1057	1470	943	210	2623	3.4188	Upchurch et al. 2004b
SMA 0009	Diplodocoidea	SMA 0009	0.1539	224.8	186.5	44.5	455.8	2.6588	Schwarz et al. 2007
Euhelopus zdanskyi	basal Macronaria	Wiman 1929 #1	0.2131	955	602	125.2	1682.2	3.2259	Carrano 1998a
Camarasaurus lentus	basal Macronaria	CM 11138	0.0670	567.5	350	88	1005.5	3.0024	pers.obs. + Carrano 1998a
Camarasaurus supremus	basal Macronaria	AMNH 5761	0.2152	1800	1040	225	3065	3.4864	Osborn and Mook 1921
Bellusaurus sui	basal Macronaria	IVPP V.83003	0.1331	480	280	92	852	2.9304	pers. obs.
Camarasaurus supremus	basal Macronaria	KUVP 129716	0.0946	1465	901	219	2585	3.4125	Bonnan 2001 + Wilhite 2003
Camarasaurus grandis	basal Macronaria	GMNH 101	0.1012	1485	930	223	2638	3.4213	McIntosh et al. 1996
Bothriospondylus madagascariensis	basal Macronaria	****	0.0376	1460	870	230	2560	3.4082	pers. obs.+ Lapparent 1943
Chubutisaurus insignis	basal Titanosauria	UNPSJB-PV 920	0.5855	1715	960	560	3235	3.5099	Martínez et al. 2004
Epachthosaurus sciuttoi	basal Titanosauria	MACN 18222	0.1154	1095	700	177	1972	3.2949	pers. obs. + Carrano 1998a
Janenschia robusta	basal Titanosauria	****	0.0784	1270	830	164	2264	3.3549	pers. obs. + Janensch 1961 + Carrano 1998a
Ligabuesaurus leanzai	basal Titanosauria	MCF-PHV-233	0.1615	1660	1040	220	2920	3.4654	Bonaparte et al. 2006
Rapetosaurus krausei	Lithostrotia	FMNH PR 2209	0.2515	594	500	89	1183	3.0730	Curry-Rogers pers.com. 2007 + Curry-Rogers and Forster 2001
Antarctosaurus wichmannianus	Lithostrotia	MACN 6804	0.0792	1405	912	208.9	2525.9	3.4024	Carrano 1998a
Laplatasaurus araukanicus	Lithostrotia	MLP-Av 1047/1128	0.2589	1000	650	225	1875	3.2730	pers. obs. + Carrano 1998a
Opisthocoelicaudia skarzynskii	Lithostrotia	ZPAL MgD I/48	0.1063	1395	810	200	2405	3.3811	Carrano 1998a
Saltasaurus robustus	Lithostrotia	CS 1480/2604	0.2361	700	400	140	1240	3.0934	Carrano 1998a
Aeolosaurus rionegrinus	Lithostrotia	MPCA 27100	0.1545	1209	813	167	2189	3.3402	Salgado et al. 1997b
Eoraptor lunensis	basal Theropoda	PVSJ 512	0.0959	152	157	81	390	2.5911	Holtz pers.com. 2006
Herrerasaurus ischigualastensis	basal Theropoda	PVL 2566	0.0388	475	410	221	1106	3.0438	pers. obs.
Herrerasaurus ischigualastensis	basal Theropoda	PVSJ 373	0.0161	352	318	164.5	834.5	2.9214	Carrano 1998a
Herrerasaurus ischigualastensis	basal Theropoda	MACN 18.060	0.0200	280.6	259	132	671.6	2.8271	Carrano 1998a
Herrerasaurus	basal Theropoda	PVL 2054	0.0051	370	335	176.1	881.1	2.9450	Carrano 1998a

ischigualastensis									
Herrerasaurus ischigualastensis	basal Theropoda	MLP 61-VIII-2-3	0.0465	336	287	154.5	777.5	2.8907	Carrano 1998a
Allosaurus fragilis	Carnosauria	YPM 4944	0.0467	526	450	238	1214	3.0842	Carrano 1998b
Allosaurus fragilis	Carnosauria	MOR 693	0.0890	742.5	706.5	346	1795	3.2541	Carrano 1998b
Allosaurus fragilis	Carnosauria	CM 11844	0.0133	842.5	724	360	1926.5	3.2848	Carrano 1998b
Allosaurus fragilis	Carnosauria	AMNH 630	0.0267	850	732	355	1937	3.2871	Carrano 1998b
Allosaurus fragilis	Carnosauria	AMNH 6125	0.0493	973	766	402	2141	3.3306	Carrano 1998b
Sinraptor dongi	Carnosauria	IVPP 10600	0.0687	876	769	410	2055	3.3128	Gatesy and Middleton 1997
Acrocanthosaurus atokensis	Carnosauria	NCSM 14345	0.1500	1277	960	439	2676	3.4275	Currie and Carpenter 2000
Allosaurus sp.	Carnosauria	AMNH 290	0.0264	985	810	423	2218	3.3460	Gatesy and Middleton 1997
Allosaurus fragilis	Carnosauria	UUVP 60001	0.0282	850	745	372	1967	3.2938	Gatesy and Middleton 1997
Allosaurus fragilis	Carnosauria	USNM 4734	0.0709	850	690	327	1867	3.2711	Gatesy and Middleton 1997
Allosaurus jimmadseni	Carnosauria	DINO 11541	0.1003	664	617	324	1605	3.2055	Holtz pers.com. 2006
Acrocanthosaurus atokensis	Carnosauria	MU 0-80-59	0.1193	1153	865	416	2434	3.3863	Gatesy and Middleton 1997
Acrocanthosaurus atokensis	Carnosauria	BHI unnumbered	0.0262	1140	930	470	2540	3.4048	Holtz pers.com. 2006
Szechuanosaurus campi	Carnosauria	IVPP V.239	0.1834	364	360	200	924	2.9657	Gatesy and Middleton 1997
Chilantaisaurus tashuikouensis	Carnosauria	IVPP V.2884.7	0.0827	1190	954	450	2594	3.4140	Gatesy and Middleton 1997
Saurophaganax maximus	Carnosauria	OMNH 01708, 01370	0.0384	1135	907	470	2512	3.4000	Holtz pers.com. 2006
Coelophysis bauri	Ceratosauria	UCMP 129618	0.0300	245	255	150	650	2.8129	Gatesy and Middleton 1997
Coelophysis bauri	Ceratosauria	AMNH 7223	0.0034	209	224	126	559	2.7474	Holtz pers.com. 2006
Coelophysis bauri	Ceratosauria	AMNH 7224	0.0279	203	221	120	544	2.7356	Holtz pers.com. 2006
Coelophysis bauri	Ceratosauria	AMNH 7249	0.0569	196	207	110	513	2.7101	Gatesy and Middleton 1997
Coelophysis bauri	Ceratosauria	AMNH 7247	0.0759	125	138	84	347	2.5403	Gatesy and Middleton 1997
Coelophysis bauri	Ceratosauria	MNA V3318	0.0694	123	136	82	341	2.5328	Gatesy and Middleton 1997
Coelophysis bauri	Ceratosauria	AMNH 7246	0.0475	122	136	79	337	2.5276	Gatesy and Middleton 1997
Coelophysis bauri	Ceratosauria	AMNH 7234	0.1151	118	135	84	337	2.5276	Gatesy and Middleton 1997
Coelophysis bauri	Ceratosauria	MNA V3318	0.0694	123	136	82	341	2.5328	Gatesy and Middleton 1997
Coelophysis bauri	Ceratosauria	AMNH 7231	0.0449	132	140	75.3	347.3	2.5407	Holtz pers.com. 2006
Dilophosaurus wetherilli	Ceratosauria	UCMP 37302	0.0862	557	580	300	1437	3.1575	Holtz pers.com. 2006
Podokesaurus holyokensis	Ceratosauria	destroyed	0.1568	86	104	65	255	2.4065	Holtz pers.com. 2006
Procompsognathus triassicus	Ceratosauria	SMNS 12591	0.1448	93	113	69	275	2.4393	Holtz pers.com. 2006
Segisaurus halli	Ceratosauria	UCMP 32101	0.0886	145	160	99	404	2.6064	Holtz pers.com. 2006
Syntarsus rhodesiensis	Ceratosauria	QG 1	0.0384	208	223	132	563	2.7505	Holtz pers.com. 2006
Ceratosaurus nasicornis	Ceratosauria	USNM 4735	0.2766	620	555	254	1429	3.1550	Holtz pers.com. 2006
Elaphrosaurus bambergi	Ceratosauria	HMN Gr. S. 38-44	0.1431	529	608	391	1528	3.1841	Holtz pers.com. 2006
Afrovenator abakensis	Ceratosauria	UC OBA 1	0.2549	760	687	321	1768	3.2475	Holtz pers.com. 2006
Eustreptospondylus oxoniensis	Ceratosauria	OUM J13558	0.2092	520	500	235	1255	3.0986	Holtz pers.com. 2006
Albertosaurus sarcophagus	Coelurosauria	ROM 807	0.1001	1020	1030	590	2640	3.4216	Holtz pers.com. 2006
Deinonychus antirrhopus	Coelurosauria	MCZ 4371	0.2340	336	382	164	882	2.9455	Gatesy and Middleton 1997
Deinonychus antirrhopus	Coelurosauria	YPM	0.1959	331	370	168	869	2.9390	Gatesy and Middleton 1997
Albertosaurus libratus	Coelurosauria	NCM 2120	0.1286	1040	1000	594	2634	3.4206	Gatesy and Middleton 1997
Albertosaurus libratus	Coelurosauria	AMNH 5458	0.1207	1025	990	625	2640	3.4216	Gatesy and Middleton 1997
Sinosauropteryx prima	Coelurosauria	NIGP 127586	0.1140	53.2	61.2	40	154.4	2.1886	Currie and Chen 2001
Sinosauropteryx prima	Coelurosauria	NIGP 127587	0.0944	86.4	96.8	62.5	245.7	2.3904	Currie and Chen 2001
Bambiraptor feinbergi	Coelurosauria	FIP 001	0.1695	119	168	78	365	2.5623	Burnham et al. 2000
Bambiraptor feinbergi	Coelurosauria	FIP uncat/AMNH 002-036	0.1462	170	225	105	500	2.6990	Holtz pers.com. 2006
Daspletosaurus torosus	Coelurosauria	NMC 350	0.1428	930	870	555	2355	3.3720	Gatesy and Middleton 1997
Dromiceiomimus brevitertius	Coelurosauria	NMC 12228	0.1913	468	578	397	1443	3.1593	Gatesy and Middleton 1997
Dromiceiomimus brevitertius	Coelurosauria	NMC 12069	0.1680	376	511	308	1195	3.0774	Gatesy and Middleton 1997
Gallimimus bullatus	Coelurosauria	GI 100/11	0.1665	660	735	520	1915	3.2822	Gatesy and Middleton 1997

Gallimimus bullatus	Coelurosauria	GI 100/10	0.1879	192	218	157	567	2.7536	Gatesy and Middleton 1997
Ornithomimus edmontonicus	Coelurosauria	ROM 851	0.0973	435	475	310	1220	3.0864	Gatesy and Middleton 1997
Struthiomimus altus	Coelurosauria	AMNH 5257	0.1379	513	560	385	1458	3.1638	Gatesy and Middleton 1997
Sinornithomimus dongi	Coelurosauria	IVPP−V11797−10	0.0851	323	335	213	871	2.9400	Kobayashi and Lü 2003
Tanycolagreus topwilsoni	Coelurosauria	TPII 2000-09-29	0.0526	356	387	216	959	2.9818	Holtz pers.com. 2006
Dilong paradoxus	Coelurosauria	IVPP V14243	0.0142	181	203	117	501	2.6998	Holtz pers.com. 2006
Appalachiosaurus montgomeriensis	Coelurosauria	RMM 6670 r	0.0754	754.7	780.7	482.2	2017.6	3.3048	Holtz pers.com. 2006
Albertosaurus sarcophagus	Coelurosauria	NMC 11315	0.1361	648	648	445	1741	3.2408	Holtz pers.com. 2006
Gorgorosaurus libratus	Coelurosauria	AMNH 5458	0.1207	1025	990	625	2640	3.4216	Holtz pers.com. 2006
Gorgorosaurus libratus	Coelurosauria	AMNH 5423	0.1443	600	630	440	1670	3.2227	Holtz pers.com. 2006
Daspletosaurus torosus	Coelurosauria	RTMP 85.62.1	0.2188	1020	857	561	2438	3.3870	Holtz pers.com. 2006
Daspletosaurus sp.	Coelurosauria	NMC 11315	0.0465	665	736	448	1849	3.2669	Holtz pers.com. 2006
Daspletosaurus sp.	Coelurosauria	OMNH 10131	0.2537	1033	891	483	2407	3.3815	Holtz pers.com. 2006
Tarbosaurus bataar	Coelurosauria	PIN 552-2	0.1438	560	781	420	1761	3.2458	Holtz pers.com. 2006
Tarbosaurus bataar	Coelurosauria	GI 107/2	0.2868	1120	885	526	2531	3.4033	Holtz pers.com. 2006
Tyrannosaurus rex	Coelurosauria	FMNH PR2081	0.1999	1345	1245	671	3261	3.5134	Holtz pers.com. 2006
Tyrannosaurus rex	Coelurosauria	BMRP2002.4.1	0.1366	720	840	560	2120	3.3263	Holtz pers.com. 2006
Struthiomimus altus	Coelurosauria	ROM 1790	0.1400	397	430	297	1124	3.0508	Holtz pers.com. 2006
Chuandongocoelurus primitivus	Coelurosauria	He 1984	0.0732	200	237	122	559	2.7474	Holtz pers.com. 2006
Caudipteryx sp.	Coelurosauria	IVPP V12430	0.1201	145	183	112	440	2.6435	Holtz pers.com. 2006
Caudipteryx zoui	Coelurosauria	NGMC 97-9-A	0.1332	149	182	117	448	2.6513	Holtz pers.com. 2006
Caudipteryx zoui	Coelurosauria	BPM 001	0.1293	145	188	113	446	2.6493	Holtz pers.com. 2006
Bambiraptor feinbergi	Coelurosauria	FIP uncat/AMNH 002-036	0.1462	170	225	105	500	2.6990	Holtz pers.com. 2006
Ornithomimus edmontonicus	Coelurosauria	RTMP uncat	0.1555	418	485	332	1235	3.0917	Holtz pers.com. 2006
Garudimimus brevipes	Coelurosauria	GI 100/13	0.0642	371	388	229	988	2.9948	Holtz pers.com. 2006
Ingenia yanshini	Coelurosauria	GI 100/30	0.1799	228	281	125	634	2.8021	Holtz pers.com. 2006
Chirostenotes pergracilis	Coelurosauria	TMP 79.30.1	0.0258	310	367	208	885	2.9469	Holtz pers.com. 2006
Ornitholestes hermanni	Coelurosauria	AMNH 619	0.1487	207	252	117	576	2.7604	Holtz pers.com. 2006
Compsognathus longipes	Coelurosauria	BSP ASI 536	0.1756	67	87.6	56	210.6	2.3235	Holtz pers.com. 2006
Compsognathus longipes	Coelurosauria	MNMH CNJ 79	0.0869	110	136	81	327	2.5145	Holtz pers.com. 2006
Beipiaosaurus inexpectatus	Coelurosauria	IVPP V11559	0.3583	265	275	107	647	2.8109	Holtz pers.com. 2006
Avimimus portentosus	Coelurosauria	PIN 3907/1	0.1659	188	257	153	598	2.7767	Holtz pers.com. 2006
Caudipteryx dongi	Coelurosauria	IVPP V12344	0.1584	152	196	124	472	2.6739	Holtz pers.com. 2006
Khaan mckennai	Coelurosauria	IGM 100/1127	0.2047	150	166	75	391	2.5922	Holtz pers.com. 2006
Oviraptorid unnamed	Coelurosauria	AMNH unnumbered	0.1391	192	225	107	524	2.7193	Holtz pers.com. 2006
Protarchaeopteryx robusta	Coelurosauria	NGMC 2125	0.0964	122	160	85	367	2.5647	Holtz pers.com. 2006
Parvicursor remotus	Coelurosauria	PIN 4487/25	0.3737	52.6	75.6	58.1	186.3	2.2702	Holtz pers.com. 2006
Shuvuuia deserti	Coelurosauria	MPD 100/120	0.4011	64	97.7	73.6	235.3	2.3716	Holtz pers.com. 2006
Mei long	Coelurosauria	IVPP V12733	0.0973	81	106	58	245	2.3892	Holtz pers.com. 2006
Saurornithoides mongoliensis	Coelurosauria	AMNH 6516	0.0587	198	243	139	580	2.7634	Holtz pers.com. 2006
Sinornithoides youngi	Coelurosauria	IVPP V9612	0.1666	140	198	111	449	2.6522	Holtz pers.com. 2006
Achillobator giganticus	Coelurosauria	MNU FR-15	0.2405	505	490.4	234.4	1229.8	3.0898	Holtz pers.com. 2006
Epidendrosaurus ningchengensis	Coelurosauria	IVPP V12653	0.0849	16.2	19.4	11.9	47.5	1.6767	Holtz pers.com. 2006
Scansoriopteryx heilmanni	Coelurosauria	CAGS 02-IG-gausa-1/DM 607	0.0822	16.5	19.25	12	47.75	1.6790	Holtz pers.com. 2006
Juravenator starki	Coelurosauria	JME Sch 200	0.0206	52	58.1	34	144.1	2.1587	Holtz pers.com. 2006
Nqwebasaurus thwazi	Coelurosauria	AM 6040	0.0697	118	140.7	72.7	331.4	2.5204	Holtz pers.com. 2006
Huaxiagnathus orientalis	Coelurosauria	CAGS IG02-301)	0.0634	167	189	117	473	2.6749	Holtz pers.com. 2006
Neimongosaurus yangi	Coelurosauria	LH V0001	0.8085	366	310	79	755	2.8779	Holtz pers.com. 2006
Microraptor zhaoianus	Coelurosauria	IVPP V12330	0.0865	53	68	38	159	2.2014	Holtz pers.com. 2006
Microraptor zhaoianus	Coelurosauria	CAGS 20-7-004	0.0759	74.4	94.14	49.39	217.93	2.3383	Holtz pers.com. 2006

Saurornitholestes langstoni	Coelurosauria	RTMP 88.121.30	0.2250	216	279	116	611	2.7860	Holtz pers.com. 2006
Velociraptor mongoliensis	Coelurosauria	IGM 100/986	0.3427	238	255	99.1	592.1	2.7724	Holtz pers.com. 2006
Archaeornithomimus asiaticus	Coelurosauria	AMNH 6565	0.2408	314	401	286	1001	3.0004	Holtz pers.com. 2006
Tanycolagreus topwilsoni	Coelurosauria	TPII 2000-09-29	0.0526	356	387	216	959	2.9818	Holtz pers.com. 2006
Dilong paradoxus	Coelurosauria	IVPP V14243	0.0142	181	203	117	501	2.6998	Holtz pers.com. 2006
Gasparinisaura cincosaltensis	Iguanodontia	MUCPV-208	0.4293	94.7	79.4	55.8	229.9	2.3615	Carrano 1998a
Tenontosaurus dossi	Iguanodontia	FWMSH 93B1	0.0842	557	565	226	1348	3.1297	Carrano 1998a
Tenontosaurus tilletti	Iguanodontia	AMNH 3022	0.1162	201.2	217	80.4	498.6	2.6978	Carrano 1998a
Tenontosaurus tilletti	Iguanodontia	MCZ 4205	0.0503	388.5	370.5	152.6	911.6	2.9598	Carrano 1998a
Tenontosaurus tilletti	Iguanodontia	AMNH 3014	0.1202	304.5	300	132	736.5	2.8672	Carrano 1998a
Saurolophus osborni	Iguanodontia	5220	0.0249	1150	1020	420	2590	3.4133	Brett-Surman 1975
Edmontosaurus annectans	Iguanodontia	YPM 2182	0.0544	1060	950	360	2370	3.3747	Brett-Surman 1975
Edmontosaurus copeia	Iguanodontia	AMNH 5730	0.1080	1356	1141	426	2923	3.4658	Brett-Surman 1975
Edmontosaurus edmontoni	Iguanodontia	NMC 2288	0.1208	1118	930	345	2393	3.3789	Brett-Surman 1975
Shantungosaurus giganteus	Iguanodontia	Cheng-Chi 1973	0.0660	1650	1448	550	3648	3.5621	Brett-Surman 1975
Kritosaurus incurvimanus	Iguanodontia	ROM 764	0.1148	1041	889	324	2254	3.3530	Brett-Surman 1975
Prosaurolophus maximus	Iguanodontia	ROM 787	0.0906	997	860	321	2178	3.3381	Brett-Surman 1975
Lambeosaurus lambei	Iguanodontia	ROM 12518	0.0973	1067	953	343	2363	3.3735	Brett-Surman 1975
Tsintaosaurus spinorhinus	Iguanodontia	PMNH V728	0.1588	1000	1050	336	2386	3.3777	Brett-Surman 1975
Camptosaurus medius	Iguanodontia	CM 11337	0.0745	395	360	158	913	2.9605	Brett-Surman 1975
Abrictosaurus consors	non-Iguanodontia	BMNH RU B.54	0.1495	77.1	102.8	53.7	233.6	2.3685	Carrano 1998a
Heterodontosaurus tucki	non-Iguanodontia	SAM K337	0.0870	113.2	140	72.9	326.1	2.5134	Carrano 1998a
Hypsilophodon foxii	non-Iguanodontia	BMNH R.5830	0.0318	101	118	58	277	2.4425	Carrano 1998a
Hypsilophodon foxii	non-Iguanodontia	BMNH R.196	0.0679	145.8	150	82.8	378.6	2.5782	Carrano 1998a
Laosaurus consors	non-Iguanodontia	YPM 1882	0.1007	246	277	125	648	2.8116	Carrano 1998a
Leaellynasaura amicagraphica	non-Iguanodontia	NMV P186047	0.2004	135	185	102	422	2.6253	Carrano 1998a
Orodromeus makelai	non-Iguanodontia	MOR 294	0.0914	103.8	103.1	54.2	261.1	2.4168	Carrano 1998a
Orodromeus makelai	non-Iguanodontia	MOR 661	0.0728	46.7	51	28.8	126.5	2.1021	Carrano 1998a
Orodromeus makelai	non-Iguanodontia	MOR 623 (1)	0.0830	45.1	52.2	29	126.3	2.1014	Carrano 1998a
Othnielia rex	non-Iguanodontia	MCZ 4454R (BYU ESM-163R)	0.1148	139.1	174.3	76	389.4	2.5904	Carrano 1998a
Parkosaurus warrenae	non-Iguanodontia	ROM 804	0.0396	270	312.5	151	733.5	2.8654	Carrano 1998a
Thescelosaurus neglectus	non-Iguanodontia	NMC 8537	0.3187	338	280	125	743	2.8710	Carrano 1998a
Xiaosaurus dashanpensis	non-Iguanodontia	IVPP V673OA	0.1079	110	118	70	298	2.4742	Carrano 1998a
Hypsilophodon foxii	non-Iguanodontia	****	0.0902	150	155	76	381	2.5809	Hulke 1882
Archaeopteryx lithographica	Aves	Eichstatt	0.1873	37	53	30	120	2.0792	Holtz pers.com. 2006
Archaeopteryx lithographica	Aves	SAV	0.2150	48	71	40.5	159.5	2.2028	Holtz pers.com. 2006
Archaeopteryx lithographica	Aves	Berlin	0.0705	52.6	68.5	36	157.1	2.1962	Holtz pers.com. 2006
Archaeopteryx lithographica	Aves	London	0.0436	60.5	80.5	40	181	2.2577	Holtz pers.com. 2006
Archaeopteryx lithographica	Aves	Solnhofen	0.0747	70	89.5	47.8	207.3	2.3166	Holtz pers.com. 2006
Confuciusornis sanctus	Aves	GMV-2130	0.0851	41.78	48.7	23.21	113.69	2.0557	Holtz pers.com. 2006
Confuciusornis sanctus	Aves	GMV-2133	0.1001	46.85	53.29	25.64	125.78	2.0996	Holtz pers.com. 2006
Confuciusornis sanctus	Aves	IVPP V11619	0.1134	47	54	25	126	2.1004	Holtz pers.com. 2006
Confuciusornis sanctus	Aves	NGMC 98-8-2	0.0695	56	65	34	155	2.1903	Holtz pers.com. 2006
Omnivoropteryx sinousaorum	Aves	CAGS02-IG-gausa-3/DM 609	0.1036	81	89.3	46.6	216.9	2.3363	Holtz pers.com. 2006
Patagopteryx deferrariisi	Aves	MACN-N-11	0.1961	99.1	136.2	50.8	286.1	2.4565	Holtz pers.com. 2006
Patagopteryx deferrariisi	Aves	MUCPv-48	0.2079	97.6	140	51	288.6	2.4603	Holtz pers.com. 2006
Rahonavis ostromi	Aves	UA 8656 r	0.1411	87.1	120.2	48.1	255.4	2.4072	Holtz pers.com. 2006
Rahonavis ostromi	Aves	UA 8656 l	0.1419	88	119.8	48	255.8	2.4079	Holtz pers.com. 2006
Sapeornis chaoyangensis	Aves	IVPP V12698l	0.1969	80.4	83.6	53.2	217.2	2.3369	Holtz pers.com. 2006

Sapeornis chaoyangensis	Aves	IVPP V13276	0.1039	72.1	85.3	48.2	205.6	2.3130	Holtz pers.com. 2006
Yanornis martini	Aves	IVPP V12558	0.1387	52	79.3	38	169.3	2.2287	Holtz pers.com. 2006
Yixianornis grabaui	Aves	IVPP V12631	0.0181	41	52	26	119	2.0755	Holtz pers.com. 2006
Ornithorhynchus anatinus	Prototheria	UMMZ uncat.	0.1765	31	47	9	87	1.9395	Gingerich 2003
Ornithorhynchus anatinus	Prototheria	FMNH 60902	0.1855	32.3	46.3	9.5	88.1	1.9450	Carrano 1998a
Tachyglossus aculeatus	Prototheria	FMNH 127265	0.3583	66.6	67	9.1	142.7	2.1544	Carrano 1998a
Monodelphis domestica	Metatheria	Jena	0.1526	27	27	7	61	1.7853	M. Schmidt, pers. com. 2006 + Schmidt 2005
Dasyuroides byrnei	Metatheria	Jena	0.4030	31	39	17	87	1.9395	M. Schmidt, pers. com. 2006 + Schmidt 2005
Didelphis virginiana	Metatheria	Mam 6562 (PMJ)	0.2775	83	78	18	179	2.2529	M. Schmidt, pers. com. 2006 + Schmidt 2005
Didelphis virginiana	Metatheria	Mam 1715 (PMJ)	0.2991	85	84	18	187	2.2718	M. Schmidt, pers. com. 2006 + Schmidt 2005
Trichosurus vulpecula	Metatheria	Mam 6560 (PMJ)	0.2962	85	82	18	185	2.2672	M. Schmidt, pers. com. 2006 + Schmidt 2005
Trichosurus vulpecula	Metatheria	Mam 819 (PMJ)	0.2201	85	82	20	187	2.2718	M. Schmidt, pers. com. 2006 + Schmidt 2005
Trichosurus vulpecula	Metatheria	Mam 1976 (PMJ)	0.2532	98	94	22	214	2.3304	M. Schmidt, pers. com. 2006 + Schmidt 2005
Isoodon obesulus	Metatheria	Jena	0.1978	47	47	17.5	111.5	2.0473	M. Schmidt, pers. com. 2006 + Schmidt 2005
Chironectes minimus	Metatheria	Mam 6552 (PMJ)	0.1205	48	50	13	111	2.0453	M. Schmidt, pers. com. 2006 + Schmidt 2005
Philander opossum	Metatheria	Mam 6598 (PMJ)	0.1093	54	60	15	129	2.1106	M. Schmidt, pers. com. 2006 + Schmidt 2005
Marmosa robinsoni	Metatheria	Mam 6588 (PMJ)	0.0975	25	27	7	59	1.7709	M. Schmidt, pers. com. 2006 + Schmidt 2005
Marmosa robinsoni	Metatheria	Mam 6584 (PMJ)	0.1052	25	28	7	60	1.7782	M. Schmidt, pers. com. 2006 + Schmidt 2005
Monodelphis sorex	Metatheria	Jena	0.1526	27	27	7	61	1.7853	M. Schmidt, pers. com. 2006 + Schmidt 2005
Macropus eugenii	Metatheria	FMNH 1'4801	0.3031	123.8	178	61	362.8	2.5597	Carrano 1998a
Macropus fuliginosus	Metatheria	FMNH 44295	0.6454	195.1	417	152.2	764.3	2.8833	Carrano 1998a
Macropus giganteus	Metatheria	FMNH 60153	0.6450	177.9	325	142.2	645.1	2.8096	Carrano 1998a
Eomaia scansoria	basal Eutheria	CAGS 01-IG-1a	0.0000	16.7	19.5	3.9	40.1	1.6031	Ji et al. 2002
Hippopotamus amphibius	Artiodactyla	FMNH 127871	0.7305	422	325	121.2	868.2	2.9386	Carrano 1998a
Giraffa camelopardalis	Artiodactyla	MCZ*	0.3842	484	560	630	1674	3.2238	Carrano 1998a
Hippopotamus amphibius	Artiodactyla	UMMZ 84041	0.8260	465	280	115	860	2.9345	Gingerich 2003
Prosynthetoceras francisi	Artiodactyla	AM 32058	0.2180	192	237	126	555	2.7443	Webb et al. 2003
Equus onager	Artiodactyla	****	0.0997	303	297	243	843	2.9258	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Equus caballus przewalski	Artiodactyla	****	0.1476	315.5	290.4	251	856.9	2.9329	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Camelus bactrianus	Artiodactyla	****	0.2336	482	382	322	1186	3.0741	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Tragulus meminna	Artiodactyla	****	0.2173	99.05	103	58.9	260.95	2.4166	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Tragulus napu	Artiodactyla	****	0.1994	87.9	96	54.5	238.4	2.3773	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Tragulus javanicus	Artiodactyla	****	0.1698	84.5	91.45	54.1	230.05	2.3618	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Tragulus sp.	Artiodactyla	****	0.0921	87.9	95	61.9	244.8	2.3888	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Okapi johnstoni	Artiodactyla	****	0.2187	321.5	327	318	966.5	2.9852	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Giraffa camelopardalis	Artiodactyla	****	0.4476	530	601	739	1870	3.2718	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Tragelaphus spekei	Artiodactyla	****	0.0273	278	313	217.2	808.2	2.9075	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Tragelaphus strepsiceros	Artiodactyla	****	0.0977	322.5	347	285	954.5	2.9798	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Tragelaphus eurycerus	Artiodactyla	****	0.1490	343	336.5	221	900.5	2.9545	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Boselaphus tragocamdus	Artiodactyla	****	0.0381	324.5	339	251	914.5	2.9612	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Bubalus bubalis	Artiodactyla	****	0.1665	376	344	240.5	960.5	2.9825	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Bison bison	Artiodactyla	****	0.1324	337	320	225.5	882.5	2.9457	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Bison bonasus	Artiodactyla	****	0.1823	426	421	262	1109	3.0449	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Cephalophus sylvicultor	Artiodactyla	****	0.1296	252.5	238	171	661.5	2.8205	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Cephalophus dorsalis	Artiodactyla	****	0.1296	152.9	142.1	105.4	400.4	2.6025	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Kobus ellipsiprymnus	Artiodactyla	****	0.0841	307	314.5	217	838.5	2.9235	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Kobus leche	Artiodactyla	****	0.0543	248.1	280.3	212.7	741.1	2.8699	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Pelea capreolus	Artiodactyla	****	0.1936	177	226.5	185	588.5	2.7697	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Hippotragus niger	Artiodactyla	****	0.0240	305	326	236	867	2.9380	K.E. Lilje pers.com. 2006 + Lilje et al. 2003

Oryx gazella	Artiodactyla	****	0.0410	284.5	300.3	228.8	813.6	2.9104	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Addax nasomaculata	Artiodactyla	****	0.0582	248.5	278	213.5	740	2.8692	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Damaliskus dorcas phillipsi	Artiodactyla	****	0.1619	215	252.5	213.5	681	2.8331	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Alcephalus buselaphus	Artiodactyla	****	0.1557	275	336	272.5	883.5	2.9462	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Connochaetes gnou	Artiodactyla	****	0.0459	257	300	216	773	2.8882	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Oreotragus oreotragus	Artiodactyla	****	0.1817	126.6	140	80.7	347.3	2.5407	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Raphicerus campestris	Artiodactyla	****	0.1421	151.5	196	145	492.5	2.6924	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Raphicerus campestris	Artiodactyla	****	0.1266	126.6	157	120	403.6	2.6060	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Madoqua saltiana	Artiodactyla	****	0.1625	97.5	126.8	96.7	321	2.5065	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Madoqua guentheri	Artiodactyla	****	0.2176	92	127.3	98.1	317.4	2.5016	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Aepyceros melampus	Artiodactyla	****	0.2238	218.5	274	238	730.5	2.8636	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Aepyceros melampus	Artiodactyla	****	0.2219	213.5	268	232	713.5	2.8534	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Litocranius walleri	Artiodactyla	****	0.2684	194	249.5	225	668.5	2.8251	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Litocranius walleri sclateri	Artiodactyla	****	0.2596	182.5	233	209	624.5	2.7955	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Gazella thomsoni	Artiodactyla	****	0.1894	161.6	201.3	167.9	530.8	2.7249	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Gazella dama	Artiodactyla	****	0.2942	226	289	271	786	2.8954	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Gazella dama mhorr	Artiodactyla	****	0.2827	230	285	270	785	2.8949	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Saiga tatarica	Artiodactyla	****	0.1642	166.5	189.3	164.1	519.9	2.7159	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Capricornis crispus	Artiodactyla	****	0.1758	212	244.5	139.5	596	2.7752	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Rupicapra rupicapra	Artiodactyla	****	0.1222	211.5	266	163	640.5	2.8065	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Rupicapra ruficeps	Artiodactyla	****	0.1166	203	261	165.5	629.5	2.7990	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Capra ibex cylindricornis	Artiodactyla	****	0.2843	236.5	272.5	136	645	2.8096	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Capra ibex	Artiodactyla	****	0.2622	242	288	146	676	2.8299	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Capra pyrenaica	Artiodactyla	****	0.1889	227	260.5	146.5	634	2.8021	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Capra hircus thibethanus	Artiodactyla	****	0.2490	196	223.5	117	536.5	2.7296	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Ammotragus lervia	Artiodactyla	****	0.1808	252	272	159	683	2.8344	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Ovis ammon orientalis	Artiodactyla	****	0.0416	192	223	153	568	2.7543	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Ovis canadensis	Artiodactyla	****	0.0464	263.5	308	210.2	781.7	2.8930	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Moschus moschiferus	Artiodactyla	****	0.1273	184	225.5	175	584.5	2.7668	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Muntiacus reevesi	Artiodactyla	****	0.0443	133.9	140.6	107.5	382	2.5821	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Muntiacus muntjac	Artiodactyla	****	0.0216	158.5	171	127	456.5	2.6594	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Dama dama	Artiodactyla	****	0.0978	273	311.5	248	832.5	2.9204	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Axis axis	Artiodactyla	****	0.0278	207	234.5	171	612.5	2.7871	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Axis porcinus	Artiodactyla	****	0.0559	183.5	197	135	515.5	2.7122	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Cervus unicolor	Artiodactyla	****	0.0866	295.2	294.6	237.5	827.3	2.9177	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Cervus nippon	Artiodactyla	****	0.1344	220.5	257	211	688.5	2.8379	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Cervus elaphus	Artiodactyla	****	0.0650	312.5	316	244.5	873	2.9410	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Pudu pudu	Artiodactyla	****	0.1611	124.5	127	79.1	330.6	2.5193	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Alces alces	Artiodactyla	****	0.1338	420.5	474.5	398	1293	3.1116	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Capreolus capreolus	Artiodactyla	****	0.1758	178.5	223.5	182	584	2.7664	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Hyrachyus agrarius	Perissodactyla	AMNH*	0.2993	254	243	110	607	2.7832	Carrano 1998a
Hyracodon nebrascensis	Perissodactyla	AMNH*	0.2731	267	220	114	601	2.7789	Carrano 1998a
Hyracodon sp.	Perissodactyla	YPM-PU*	0.7225	550	435	410	1395	3.1446	Carrano 1998a
Metamynodon planifrons	Perissodactyla	AMNH*	0.1393	480	280	118	878	2.9435	Carrano 1998a
Teleoceras fossiger	Perissodactyla	AMNH*	0.1395	408	233	105	746	2.8727	Carrano 1998a
Elephas maximus	Perissodactyla	FMNH 60601	0.7115	1192	710	135.5	2037.5	3.3091	Carrano 1998a
Elephas maximus	Perissodactyla	FMNH 49894	0.3231	1025	655	193.5	1873.5	3.2727	Carrano 1998a
Elephas maximus	Perissodactyla	YPM 4009	0.1121	535	325	135	995	2.9978	Carrano 1998a
Hexaprotodon liberiensis	Perissodactyla	L-1952.4.1.4/1914.6.21.1	0.0203	277.5	190	78.3	545.8	2.7370	Gingerich 2003

Mammut americanus	Perissodactyla	AMNH	0.7565	1020	705	117	1842	3.2653	Carrano 1998a
Tapirus terrestris	Perissodactyla	UMMZ 160907	0.1655	310	235	113.5	658.5	2.8186	Gingerich 2003
Tapirus bairdii	Perissodactyla	UMMZ 81051	0.1275	325	245	113	683	2.8344	Gingerich 2003
Tapirus indicus	Perissodactyla	L-85.808	0.1551	327	260	118	705	2.8482	Gingerich 2003
Aktautitan hippopotamopus	Perissodactyla	KAN N2/875 + N2/873	0.2607	510	350	107	967	2.9854	Mihlbachler et al. 2004
Tapirus indicus	Perissodactyla	****	0.1816	320	258	120	698	2.8439	Mihlbachler et al. 2004
Palaeosyops paludosis	Perissodactyla	AMNH 11689	0.1026	355	285	111	751	2.8756	Mihlbachler et al. 2004
Dolichorhinus hyognathus	Perissodactyla	CM 11071	0.0466	457	335	132	924	2.9657	Mihlbachler et al. 2004
Rhinotitan mongoliensis	Perissodactyla	IVPPV3254	0.0170	685	465	198	1348	3.1297	Mihlbachler et al. 2004
Brontops robustus	Perissodactyla	YPM 12048	0.1676	812	448	200	1460	3.1644	Mihlbachler et al. 2004
Hyrachyus agrarius	Perissodactyla	AMNH 5065	0.2993	254	243	110	607	2.7832	Mihlbachler et al. 2004
Hyracodon nebrascensis	Perissodactyla	****	0.2731	267	220	114	601	2.7789	Mihlbachler et al. 2004
Metamynodon planifrons	Perissodactyla	AMNH 546	0.1393	480	280	118	878	2.9435	Mihlbachler et al. 2004
Menoceras arikarense	Perissodactyla	AMNH (Agate Springs)	0.2250	327	290	128	745	2.8722	Mihlbachler et al. 2004
Chilotherium anderssoni	Perissodactyla	****	0.0899	430	278	110	818	2.9128	Mihlbachler et al. 2004
Aphelops malacorhinus	Perissodactyla	FLMNH (Love Bone Bed)	0.0290	476	343	143	962	2.9832	Mihlbachler et al. 2004
Teleoceras proterum	Perissodactyla	AMNH (Mixson's Bone Bed)	0.2713	415	202	89	706	2.8488	Mihlbachler et al. 2004
Dicerorhinus sumatrensis	Perissodactyla	NMNH 49561	0.1433	478	282	142	902	2.9552	Mihlbachler et al. 2004
Rhinoceros sondiacus	Perissodactyla	NMNH 269392	0.0904	426	285	135	846	2.9274	Mihlbachler et al. 2004
Rhinoceros unicornis	Perissodactyla	NMNH 269392	0.1583	520	341	177	1038	3.0162	Mihlbachler et al. 2004
Diceros bicornis	Perissodactyla	NMNH 162935	0.1467	464	330	163	957	2.9809	Mihlbachler et al. 2004
Ceratotherium simum	Perissodactyla	NMNH 164635	0.1105	520	354	171	1045	3.0191	Mihlbachler et al. 2004
Hexaprotodon liberiensis	Perissodactyla	NMNH 581892	0.0495	277	200	78	555	2.7443	Mihlbachler et al. 2004
Toxodon burmeisteri	Perissodactyla	AMNH 14943	0.3597	577	325	101	1003	3.0013	Mihlbachler et al. 2004
Dromicosuchus grallator	Crocodylomorpha	****	0.0667	144	130	49.3	323.3	2.5096	Sues et al. 2003
Protosuchus richardsoni	Crocodylomorpha	AMNH 3024	0.0667	100	83	38	221	2.3444	Colbert and Mook 1951

Fore limb

Species	Taxa	Label	Intragroup A.D	H	R	MC III	fore length	Log fore	Reference
Lagosuchus talampayensis	Dinosauromorpha	UPLR 09	0.0000	28	18	24	70	1.8451	Sereno and Arcucci 1994
Lufengosaurus magnus	Plateosauria	IVPP V.82	0.0182	425	213	102	740	2.8692	Young 1947
Lufengosaurus huenei	Plateosauria	IVPP V.15	0.0225	335	190	80	605	2.7818	pers. obs.
Plateosaurus engelhardi	Plateosauria	HMN Skelett VI	0.0396	410	210	90	710	2.8513	pers. obs.
Plateosaurus trossingensis	Plateosauria	BMNH R.5478	0.0108	420	235	92	747	2.8733	pers. obs.
Massospondylus carinatus	Plateosauria	BP/1/5347A	0.0460	9.82	6.47	2.16	18.45	1.2660	Reisz et al. 2005
Anchisaurus polyzelus	Sauropodiformes	YPM 1883	0.0990	150	95	34	279	2.4456	Galton 1976
Gyposaurus sinensis	Sauropodiformes	IVPP V.43	0.0901	133	72	20	225	2.3522	P. Upchurch pers. com. 2006 + Young 1948
Jingshanosaurus xinwaensis	Sauropodiformes	LV003	0.0365	455	280	88	823	2.9154	pers. obs. 2006
Yunnanosaurus huangi	Sauropodiformes	IVPP AS V.20	0.0936	231	157	48	436	2.6395	pers. obs. 2006+ Young 1942
Melanorosaurus readi	Sauropodiformes	NM QR3314	0.1390	430	200	65	695	2.8420	Bonnan and Yates 2007
Vulcanodon karibaensis	non-Eusauropoda	QG 24	0.0000	700	647	206	1553	3.1912	Raath 1972 in Yates and Kitching 2003, table 1
Patagosaurus fariasi	non-Neosauropoda	PVL 4076	0.1134	1000	660	290	1950	3.2900	S. Apesteguia pers. com. 2007
Omeisaurus tianfuensis	non-Neosauropoda	ZDM T5701/5005	0.1273	1090	770	245	2105	3.3233	pers. obs.
Omeisaurus tianfuensis	non-Neosauropoda	IVPP T5704	0.1253	1040	771	244	2055	3.3128	Carrano 1998a + I. Takejiri pers. com. 2007
Shunosaurus lii	non-Neosauropoda	ZDM T5402	0.0488	670	480	170	1320	3.1206	pers. obs. + Zhang 1988
Turiasaurus riodevensis	non-Neosauropoda	CPT-1195 to 1210	0.0387	1790	1180	435	3405	3.5321	Royo-Torres et al. 2006
Mamenchisaurus guangyuanensis	non-Neosauropoda	CDUTM small specimen	0.0477	455	297	120	872	2.9405	pers. obs.
Hudiesaurus sinojapanorum	non-Neosauropoda	IVPP V. 11120	0.0715	1210	790	330	2330	3.3674	pers. obs.
Ferganasaurus verzilini	non-Neosauropoda	PIN N 3042/1	0.0860	890	580	247	1717	3.2348	Alifanov and Averianov 2003

Amargasaurus cazaui	Diplodocoidea	MACN PV N15	0.1967	705	440	230.4	1375.4	3.1384	pers. obs.
Apatosaurus louisae	Diplodocoidea	CM 3018	0.0628	1150	800	293	2243	3.3508	pers. obs.+ Gilmore 1936 + Bonnan 2001
Apatosaurus excelsus	Diplodocoidea	CM 563	0.0415	1100	755	285	2140	3.3304	pers. obs.
Apatosaurus yahnahpin	Diplodocoidea	TATE 001	0.0632	1020	646	282	1948	3.2896	Bonnan 2003
Diplodocus hayi	Diplodocoidea	CM 662/HMNS 175	0.1912	875	654	200	1729	3.2378	Bonnan 2003
Apatosaurus ajax	Diplodocoidea	NSMT-PV 20375	0.1602	1033	616	309	1958	3.2918	Upchurch et al. 2004b
SMA 0009	Diplodocoidea	SMA 0009	0.1197	181.6	134.1	45.3	361	2.5575	Schwarz et al. 2007
Brachiosaurus brancai	basal Macronaria	HMN SII	0.0792	2130	1240	620	3990	3.6010	pers. obs.
Bellusaurus sui	basal Macronaria	IVPP V.83003	0.2536	365	240	80	685	2.8357	pers. obs.
Camarasaurus supremus	basal Macronaria	KUVP 129716	0.0336	1120	745	348	2213	3.3450	Bonnan 2003 + Wilhite 2003
Bothriospondylus madagascariensis	basal Macronaria	MAA 164	0.1479	515	364	188	1067	3.0282	pers. obs.
Bothriospondylus madagascariensis	basal Macronaria	****	0.0165	1330	880	398	2608	3.4163	pers. obs. + Lapparent 1943
Camarasaurus sp.	basal Macronaria	AMNH 664	0.0762	770	472	241	1483	3.1711	Bonnan 2003
Epachthosaurus sciuttoi	basal Titanosauria	UNPSJB-PV 920	0.0347	885	530	295	1710	3.2330	Martínez et al. 2004
Argyrosaurus superbus	basal Titanosauria	MLP 77-V-29-1	0.0347	1250	820	450	2520	3.4014	S. Apesteguia pers. com. + Carrano 1998a
Rapetosaurus krausei	Lithostrotia	FMNH PR 2209	0.1947	438	324	184	946	2.9759	Curry-Rogers pers. com. 2006
Laplatasaurus araukanicus	Lithostrotia	Av. 1046*	0.1677	900	580	240	1720	3.2355	pers. obs. + Carrano 1998a + Huene 1929
Opisthocoelicaudia skarzynskii	Lithostrotia	ZPAL MgD I/48	0.1369	1000	637	275	1912	3.2815	Carrano 1998b
Alamosaurus sanjuanensis	Lithostrotia	NHNH15560	0.0491	1360	800	408	2568	3.4096	S. Apesteguia pers. com. 2007
Aeolosaurus rionegrinus	Lithostrotia	MPCA 27100	0.0896	1035	580	295	1910	3.2810	Salgado et al. 1997b
Neuquensaurus australis	Lithostrotia	CS 1100	0.2460	520	295	213.2	1028.2	3.0121	S. Apesteguia pers. com. 2007
Eoraptor lunensis	basal Theropoda	PVSJ 512	0.0908	85	63	21	169	2.2279	T. Holtz pers. com. 2006
Herrerasaurus ischigualastensis	basal Theropoda	PVSJ 373	0.0908	181.6	152	58	391.6	2.5928	Novas 1993 + Carrano 1998b
Acrocanthosaurus atokensis	Carnosauria	NCSM 14345	0.0000	370	220	89	679	2.8319	Currie and Carpenter 2000
Dilophosaurus wetherilli	Ceratosauria	UCMP 37302	0.1437	270	192	105	567	2.7536	Holtz pers.com. 2006
Syntarsus rhodesiensis	Ceratosauria	QG 1	0.1361	100	61	26	187	2.2718	Holtz pers.com. 2006
Struthiomimus altus	Coelurosauria	UCMZ(VP)1980.1	0.0817	362	239	109	710	2.8513	Nicholls and Russell 1985
Albertosaurus libratus	Coelurosauria	UCMP 37302	0.1784	324	156	98	578	2.7619	Gatesy and Middleton 1997
Sinosauropteryx prima	Coelurosauria	NIGP 127586	0.1193	22.5	12.5	7.5	42.5	1.6284	Currie and Chen 2001
Sinosauropteryx prima	Coelurosauria	NIGP 127587	0.1700	40.9	22.2	14.3	77.4	1.8887	Currie and Chen 2001
Sinornithomimus dongi	Coelurosauria	IVPP−V11797−10	0.2218	212	145	53.8	410.8	2.6136	Kobayashi and Lü 2003
Falcarius utahensis	Coelurosauria	UMNH VP 12284	0.1588	255	184	76	515	2.7118	Zanno 2006
Saurolophus osborni	Iguanodontia	AMNH 5220	0.1934	610	620	330	1560	3.1931	Brett-Surman 1975
Edmontosaurus annectans	Iguanodontia	YPM 2182	0.0883	590	550	270	1410	3.1492	Brett-Surman 1975
Edmontosaurus copeia	Iguanodontia	AMNH 5730	0.2778	617	623	370	1610	3.2068	Brett-Surman 1975
Edmontosaurus edmontoni	Iguanodontia	NMC 2288	0.0801	587	610	272	1469	3.1670	Brett-Surman 1975
Shantungosaurus giganteus	Iguanodontia	****	0.0941	1020	852	398	2270	3.3560	Brett-Surman 1975
Kritosaurus incurvimanus	Iguanodontia	ROM 764	0.0606	597	559	229	1385	3.1414	Brett-Surman 1975
Prosaurolophus maximus	Iguanodontia	ROM 787	0.1008	533	473	238	1244	3.0948	Brett-Surman 1975
Lambeosaurus lambei	Iguanodontia	ROM 12518	0.1517	521	610	254	1385	3.1414	Brett-Surman 1975
Tsintaosaurus spinorhinus	Iguanodontia	PMNH V728	0.2746	612	752	224	1588	3.2009	Brett-Surman 1975
Camptosaurus medius	Iguanodontia	CM 11337	0.5258	227	143	45	415	2.6180	Brett-Surman 1975
Parasaurolophus walkeri	Iguanodontia	ROMP 4578	0.0325	520	496	208	1224	3.0878	Lull and Wright 1942
Hypsilophodon foxii	non-Iguanodontia	****	0.0000	95	78	19	192	2.2833	Hulke 1882
Ornithorhynchus anatinus	Prototheria	UMMZ uncat.	0.0000	27.4	27.4	8.9	63.7	1.8041	Gingerich 2003
Monodelphis sorex	Metatheria	ZMB 35515	0.1717	16.6	14.4	3.5	34.5	1.5378	Molinero 2004
Dasyuroides byrnei	Metatheria	****	0.0639	26	30	7	63	1.7993	M. Schmidt pers. com. 2006 + Schmidt 2005
Sminthopsis crassicaudata	Metatheria	ZMB 32389	0.1840	11.8	15.1	2.6	29.5	1.4698	Molinero 2004
Monodelphis sorex	Metatheria	****	0.0732	22	22	5	49	1.6902	M. Schmidt pers. com. 2006
Marmosa sp. IP-FUB 26	Metatheria	IP-FUB 26	0.0308	17.7	18.7	4.3	40.7	1.6096	Molinero 2004

Sthenurus stirlingi	Metatheria	SAM P22533	0.0398	256.5	273	64.4	593.9	2.7737	Wells and Tedford 1995
Sthenurus andersoni	Metatheria	SAM P13673	0.0882	151.8	176.6	34.8	363.2	2.5601	Wells and Tedford 1995
Tachyglossus aculeatus	Metatheria	M9532	0.1956	48.9	46.9	13.8	109.6	2.0398	N. Milne pers. com. 2006
Dasycerus cristacaudata	Metatheria	M5410	0.6223	17.2	45.6	6.2	69	1.8388	N. Milne pers. com. 2006
Dasyurus geoffrori	Metatheria	M6907	0.1337	64	61.9	13.1	139	2.1430	N. Milne pers. com. 2006
Dasyurus hallucatus	Metatheria	M15817	0.2519	46.6	40.3	8.1	95	1.9777	N. Milne pers. com. 2006
Phascogale tapoatafa	Metatheria	****	0.1940	30.2	32.5	9.3	72	1.8573	N. Milne pers. com. 2006
Sarcophilis harissii	Metatheria	M16593	0.1988	97.9	99.1	29.1	226.1	2.3543	N. Milne pers. com. 2006
Thylocine cynocephalus	Metatheria	M3316	0.1398	167.5	154.2	40.4	362.1	2.5588	N. Milne pers. com. 2006
Myrmecobius fasciculatus	Metatheria	M11018	0.3577	33.3	34.2	12.2	79.7	1.9015	N. Milne pers. com. 2006
Isodon obesulus	Metatheria	M6560	0.2901	48.5	40.3	13.4	102.2	2.0095	N. Milne pers. com. 2006
Parameles gunnii	Metatheria	M16590	0.1267	45.3	43.8	11.6	100.7	2.0030	N. Milne pers. com. 2006
Macrotis lagotis	Metatheria	M16102	0.3581	50.9	53.9	19	123.8	2.0927	N. Milne pers. com. 2006
Phascolactus cinereus	Metatheria	M7953	0.1239	129.6	140.7	36.8	307.1	2.4873	N. Milne pers. com. 2006
Lasiorhinus latifrons	Metatheria	M924	0.1545	112.7	103.5	22.8	239	2.3784	N. Milne pers. com. 2006
Bettongia lesueur	Metatheria	M19074	0.0643	31.8	35.4	8.5	75.7	1.8791	N. Milne pers. com. 2006
Dendrolagus matschei	Metatheria	M2252	0.0776	98.9	97.7	22.9	219.5	2.3414	N. Milne pers. com. 2006
Lagorchestes conspicillatus	Metatheria	M6733	0.2258	43.1	57.8	9.4	110.3	2.0426	N. Milne pers. com. 2006
Macropus agilis	Metatheria	M11640	0.2072	86.4	117.6	19.8	223.8	2.3499	N. Milne pers. com. 2006
Macropus eugenii	Metatheria	M6573	0.1980	56.9	74	12.5	143.4	2.1565	N. Milne pers. com. 2006
Macropus fuliginosus	Metatheria	M16203	0.1614	108.5	146.3	26.9	281.7	2.4498	N. Milne pers. com. 2006
Petrogale brachiotis	Metatheria	M198880	0.1673	51.2	62.4	11	124.6	2.0955	N. Milne pers. com. 2006
Setonis brachiotus	Metatheria	M51202	0.0758	50.7	62.2	13.1	126	2.1004	N. Milne pers. com. 2006
Thylogale sp	Metatheria	M16211	0.2032	70.6	85.6	14.4	170.6	2.2320	N. Milne pers. com. 2006
Phalanger maculatus	Metatheria	m19077	0.1145	70.2	70.3	14.7	155.2	2.1909	N. Milne pers. com. 2006
Tricosurus vulpecula	Metatheria	M10906	0.1338	68.6	76.4	14.4	159.4	2.2025	N. Milne pers. com. 2006
Wyulda squamicaudata	Metatheria	M23221	0.0885	50.6	51.5	11	113.1	2.0535	N. Milne pers. com. 2006
Eomaia scansoria	basal Eutheria	CAGS 01-IG-1a	0.1706	15	14.8	2.9	32.7	1.5145	Ji et al. 2002
Fruitafossor windscheffeli	basal Eutheria	LACM 150948	0.1706	9.2	7.6	2.4	19.2	1.2833	Luo and Wible 2005
Hippopotamus amphibius	Artiodactyla	UMMZ 84041	0.6698	350	245	125	720	2.8573	Gingerich 2003
Prosynthetoceras francisi	Artiodactyla	AM 32058	0.2526	165	185	112	462	2.6646	Webb et al. 2003
Equus onager	Artiodactyla	****	0.1270	222.6	291	207.9	721.5	2.8582	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Equus caballus przewalski	Artiodactyla	****	0.1000	241.5	296	213.7	751.2	2.8758	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Camelus bactrianus	Artiodactyla	****	0.0963	361	442	321	1124	3.0508	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Tragulus meminna	Artiodactyla	****	0.4353	76.1	60.3	37.9	174.3	2.2413	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Tragulus napu	Artiodactyla	****	0.2644	66.6	61.9	42.2	170.7	2.2322	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Tragulus javanicus	Artiodactyla	****	0.3959	68.2	55	35.95	159.15	2.2018	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Tragulus sp.	Artiodactyla	****	0.2806	68.7	60.9	42.6	172.2	2.2360	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Okapi johnstoni	Artiodactyla	****	0.0603	305	362.5	304	971.5	2.9874	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Giraffa camelopardalis	Artiodactyla	****	0.3624	483	795	720	1998	3.3006	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Tragelaphus spekei	Artiodactyla	****	0.0865	215.6	218.1	202.6	636.3	2.8037	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Tragelaphus strepsiceros	Artiodactyla	****	0.1594	248.5	291	284	823.5	2.9157	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Tragelaphus eurycerus	Artiodactyla	****	0.0990	252	250.5	204	706.5	2.8491	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Boselaphus tragocamdus	Artiodactyla	****	0.0760	247.5	299	252	798.5	2.9023	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Bubalus bubalis	Artiodactyla	****	0.1137	286.5	300	225	811.5	2.9093	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Bison bison	Artiodactyla	****	0.2508	266	301.5	182	749.5	2.8748	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Bison bonasus	Artiodactyla	****	0.2450	322	345	216	883	2.9460	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Cephalophus sylvicultor	Artiodactyla	****	0.0982	188.5	183	158	529.5	2.7239	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Cephalophus dorsalis	Artiodactyla	****	0.1140	110.9	106.2	89.9	307	2.4871	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Kobus ellipsiprymnus	Artiodactyla	****	0.0740	220	247.5	223	690.5	2.8392	K.E. Lilje pers.com. 2006 + Lilje et al. 2003

Kobus leche	Artiodactyla	****	0.1775	173.7	202.3	202.7	578.7	2.7625	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Pelea capreolus	Artiodactyla	****	0.2925	129.5	171	180	480.5	2.6817	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Hippotragus niger	Artiodactyla	****	0.0910	244	308.5	240	792.5	2.8990	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Oryx gazella	Artiodactyla	****	0.1061	217.8	281.3	216.4	715.5	2.8546	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Addax nasomaculata	Artiodactyla	****	0.1094	193	250	188	631	2.8000	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Damaliskus dorcas phillipsi	Artiodactyla	****	0.2219	167	235	207	609	2.7846	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Alcephalus buselaphus	Artiodactyla	****	0.2207	216.5	310	265	791.5	2.8985	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Connochaetes gnou	Artiodactyla	****	0.1254	211.5	275	196	682.5	2.8341	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Oreotragus oreotragus	Artiodactyla	****	0.2031	105.55	91.25	76	272.8	2.4358	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Raphicerus campestris	Artiodactyla	****	0.2165	109.5	130	135	374.5	2.5735	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Madoqua saltiana	Artiodactyla	****	0.1411	73.75	83.75	81.5	239	2.3784	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Madoqua guentheri	Artiodactyla	****	0.2213	69.7	86	87.3	243	2.3856	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Aepyceros melampus	Artiodactyla	****	0.2963	165	226	231	622	2.7938	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Aepyceros melampus	Artiodactyla	****	0.3091	157.5	215	224.5	597	2.7760	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Litocranius walleri	Artiodactyla	****	0.4390	155	205.5	261	621.5	2.7934	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Litocranius walleri sclateri	Artiodactyla	****	0.4074	148.5	193	239	580.5	2.7638	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Gazella thomsoni	Artiodactyla	****	0.3178	115.3	148.2	165	428.5	2.6320	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Gazella dama	Artiodactyla	****	0.3561	176	246.5	268	690.5	2.8392	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Gazella dama mhorr	Artiodactyla	****	0.3530	178	256	270	704	2.8476	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Saiga tatarica	Artiodactyla	****	0.1594	129.7	162.8	149.6	442.1	2.6455	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Capricornis crispus	Artiodactyla	****	0.1642	178	178.5	130	486.5	2.6871	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Rupicapra rupicapra	Artiodactyla	****	0.0724	175.5	194	147.5	517	2.7135	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Rupicapra ruficeps	Artiodactyla	****	0.0567	172	189	147	508	2.7059	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Capra ibex cylindricornis	Artiodactyla	****	0.2026	188.5	203	133.5	525	2.7202	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Capra ibex	Artiodactyla	****	0.1947	200.5	204.5	141	546	2.7372	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Capra pyrenaica	Artiodactyla	****	0.1529	181	191.5	135.5	508	2.7059	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Capra hircus thibethanus	Artiodactyla	****	0.2326	166.5	169.5	111.5	447.5	2.6508	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Ammotragus lervia	Artiodactyla	****	0.1525	202.5	223	154	579.5	2.7631	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Ovis ammon orientalis	Artiodactyla	****	0.0681	144	167.5	146	457.5	2.6604	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Ovis canadensis	Artiodactyla	****	0.0600	196.2	233.1	195.5	624.8	2.7957	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Moschus moschiferus	Artiodactyla	****	0.0984	141	146	139	426	2.6294	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Muntiacus reevesi	Artiodactyla	****	0.1433	102.7	95.1	80	277.8	2.4437	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Muntiacus muntjac	Artiodactyla	****	0.1208	121.5	114	101	336.5	2.5270	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Dama dama	Artiodactyla	****	0.0935	207.5	235	216	658.5	2.8186	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Axis axis	Artiodactyla	****	0.0818	156.5	169	156.5	482	2.6830	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Axis porcinus	Artiodactyla	****	0.1008	133.3	128.5	114.5	376.3	2.5755	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Cervus unicolor	Artiodactyla	****	0.0917	220.1	226.2	213.1	659.4	2.8191	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Cervus nippon	Artiodactyla	****	0.1282	175	187.5	184.5	547	2.7380	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Cervus elaphus	Artiodactyla	****	0.0624	241.8	287.4	242	771.2	2.8872	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Pudu pudu	Artiodactyla	****	0.3733	101.2	81.7	55.2	238.1	2.3768	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Alces alces	Artiodactyla	****	0.0034	374	414	343	1131	3.0535	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Capreolus capreolus	Artiodactyla	****	0.1268	138.5	159	151	448.5	2.6518	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Capreolus capreolus	Artiodactyla	****	0.1424	134	154	149	437	2.6405	K.E. Lilje pers.com. 2006 + Lilje et al. 2003
Tapirus terrestris	Perissodactyla	UMMZ 160907	0.0634	245	205	112.5	562.5	2.7501	Gingerich 2003
Tapirus bairdii	Perissodactyla	UMMZ 81051	0.0106	250	215	109	574	2.7589	Gingerich 2003
Tapirus indicus	Perissodactyla	L-85.808	0.0794	255	215	120	590	2.7709	Gingerich 2003
Aktautitan hippopotamopus	Perissodactyla	KAN N2/875 + N2/873	0.3053	440	280	124	844	2.9263	Mihlbachler et al. 2004
Tapirus indicus	Perissodactyla	****	0.0792	250	228	120	598	2.7767	Mihlbachler et al. 2004
Palaeosyops paludosis	Perissodactyla	AMNH 11689	0.1028	293	228	109	630	2.7993	Mihlbachler et al. 2004

Dolichorhinus hyognathus	Perissodactyla	CM 11071	0.1808	340	328	128	796	2.9009	Mihlbachler et al. 2004
Rhinotitan mongoliensis	Perissodactyla	IVPPV3254	0.1220	497	480	205	1182	3.0726	Mihlbachler et al. 2004
Brontops robustus	Perissodactyla	YPM 12048	0.0944	608	504	230	1342	3.1278	Mihlbachler et al. 2004
Hyrachyus agrarius	Perissodactyla	AMNH 5065	0.1136	197	197	93	487	2.6875	Mihlbachler et al. 2004
Hyracodon nebrascensis	Perissodactyla	****	0.1996	202	210	114	526	2.7210	Mihlbachler et al. 2004
Metamynodon planifrons	Perissodactyla	AMNH 546	0.0696	393	320	153	866	2.9375	Mihlbachler et al. 2004
Menoceras arikarense	Perissodactyla	AMNH (Agate Springs)	0.1919	244	253	136	633	2.8014	Mihlbachler et al. 2004
Chilotherium anderssoni	Perissodactyla	****	0.1187	349	280	127	756	2.8785	Mihlbachler et al. 2004
Aphelops malacorhinus	Perissodactyla	FLMNH (Love Bone Bed)	0.0552	384	345	178	907	2.9576	Mihlbachler et al. 2004
Teleoceras proterum	Perissodactyla	AMNH (Mixson's Bone Bed)	0.1619	310	240	106	656	2.8169	Mihlbachler et al. 2004
Dicerorhinus sumatrensis	Perissodactyla	NMNH 49561	0.1342	330	275	165	770	2.8865	Mihlbachler et al. 2004
Rhinoceros sondiacus	Perissodactyla	NMNH 269392	0.0670	352	289	160	801	2.9036	Mihlbachler et al. 2004
Rhinoceros unicornis	Perissodactyla	NMNH 269392	0.1795	405	340	215	960	2.9823	Mihlbachler et al. 2004
Diceros bicornis	Perissodactyla	NMNH 162935	0.1499	373	392	183	948	2.9768	Mihlbachler et al. 2004
Ceratotherium simum	Perissodactyla	NMNH 164635	0.0826	407	375	196	978	2.9903	Mihlbachler et al. 2004
Hexaprotodon liberiensis	Perissodactyla	NMNH 581892	0.1283	219	156	88	463	2.6656	Mihlbachler et al. 2004
Hexaprotodon liberiensis	Perissodactyla	L-1952.4.1.4/1914.6.21.1	0.1317	216.5	152.5	86.5	455.5	2.6585	Gingerich 2003
Toxodon burmeisteri	Perissodactyla	AMNH 14943	0.0929	387	298	147	832	2.9201	Mihlbachler et al. 2004
Hesperosuchus agilis	Crocodylomorpha	CM 29894	0.0000	138	107	127	372	2.5705	Clark et al. 2000